CONVERGENT EVOLUTION AMONG DESERT RODENTS: A GLOBAL PERSPECTIVE

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ABSTRACT

The biogeographic histories of New and Old World deserts are discussed from the viewpoints of small mammal adaptation to aridity and the development of small mammal communities in deserts. Morphoecological characteristics of rodents are compared between deserts using multivariate statistical techniques. In one analysis, Sonoran and Iranian (Kavir) rodents are shown to be more similar to one another than are the more closely phylogenetically related rodents of the Sonoran and Monte deserts of the New World. It is proposed that the rodents in the two northern deserts have had a longer time to adapt to arid conditions than have those of the Monte, thus convergent evolution is more pronounced between them. Nevertheless certain suites of traits (that is, locomotion and trophic characteristics) are associated in reversed ways among some species in the more ecologically similar deserts; parts of the "niche" of these species have been switched.

A comprehensive analysis of most genera of desert rodents from all major deserts of the world reveals that species of the Argentine Monte Desert are quite distinct from those of the other deserts, particularly in their lack of specialized traits for desert life. Species in the deserts of North America and Africa are more similar ecologically to each other than they are to species in the deserts of Asia and Australia. Cluster analysis of all species reveals that there are a limited number of roles filled by rodents in deserts. Thus, despite varying genetic background and biogeographic histories, small mammals in deserts evolve in such a manner that they can be placed into a very limited number of guilds. Moreover, these limited guilds are largely repeated within each major desert region. Thus, there is pronounced convergent evolution evident in morphology and ecology of the world's desert rodents.

INTRODUCTION

The earth supports many and varied habitats which are largely a result of the complex interactions of isolation, wind and water currents, precipitation, topography, and the distribution of land masses. The overriding factor, however, is that the earth is an essentially spherical planet, tilted slightly on its polar axis, rotating at roughly a fixed distance from the sun. Indeed, as Beaty (1978) pointed out, given the earth's shape and orbit, it was easier for Wegener to hypothesize the movement of the seemingly immutable continents than it was to suggest a general shift in the earth's climatic belts in order to account for the obvious climatic changes evident in the geological and paleontological record. While climate may vary from point to point over time (and vary greatly), and while glacial periods may wax and wane, dry areas have probably always been a part of the climatological mosaic of the biosphere (Axelrod, 1950, 1972). Because xeric areas occur in a disjunct manner around the world on continents that have had varied geological and biological histories (Fig. 1), they form a unique series of ecosystems sharing many climatological traits that are ideal for studying various facets of the evolutionary process.

In this paper I will examine how groups of largely unrelated rodents have adapted to the various deserts of the world. In some cases, the similarities of the adaptive strategies utilized are remarkable, considering the vastly different gene pools from which they were independently derived, while in other cases similar problems have been solved utilizing different adaptations.

DESERT RODENTS: COLONIZATION, ADAPTATION, AND CONVERGENT EVOLUTION

During the Permian, a supercontinent (Pangaea) existed which was composed of all of the earth's land masses. Over time this continent was fractured until a number of isolated continents were formed, with the current pattern of continents appearing only in the Cenozoic, although present-day land connections between North and South America were not completed until the late Pliocene (Dietz and Holden, 1970; Haffer, 1970; Molner and Tapponnier, 1975). For the majority of mammals, whose evolution was only just beginning in the Cretaceous, the breakup of Pangaea had little effect on their biogeographic history (Cracraft, 1974). Present-day mammals evolved from early ancestors which were either isolated on one or more of the continental sections which broke off of the first land mass, or which had to colonize the continents as they reached their current locations. This means that adaptation by mammals to arid regions probably began only in the middle to later Cenozoic (see for example, Simpson, 1961; Romer, 1966; Lundelius and Turnbull, 1967; Riek, 1970; Keast, 1972a, 1972b; Cooke, 1972; Patterson and Pascual, 1972).

The world's deserts, as we know them today, vary in topography and certain climatic features. Generally, however, they attained their pronounced levels of aridity with the orogenic activity of the Miocene and Pliocene (see for example, Furon, 1941, 1960; Axelrod, 1950, 1956, 1957, 1958, 1967, 1970, 1972; Choubert, 1952; Vuilleumier, 1971; Cooke, 1972; Bailey et al., 1977). As mountain mas-

sifs were lifted above the landscape, wind currents were disrupted, rain shadows were created, water runoff into enclosed basins led to leaching and the formation of salt lakes, primary productivity decreased with a concomitant decrease in plant cover (thus increasing the surface albedo resulting in a further decrease in rainfall), and high deserts, such as the puna of South America, were formed (Logan, 1968; Vuilleumier, 1971; Otterman, 1974; Charney et al., 1975). In all cases these climatic changes were initially gradual, occurring over millions of years, and thus allowing gradual change by vegetational communities and their associated fauna. In North and South America, for example, the transition from rather mesic forest through grassland and thorn scrub to desert has been well documented (Axelrod, 1958; Patterson and Pascual, 1972; Solbrig, 1976). Indeed, the major deserts of the world appear to have developed their extreme aridity over a time span of 20 million years or more. Although it is known that there have been significant climatic fluctuations in the past (particularly in the Pleistocene), and while these have probably had a great effect on mammalian speciation patterns, desert plants and animals are largely the result of a slow evolution through time from a period of greater moisture to one of a moisture deficit (Martin and Mehringer, 1965; Hubbard, 1974; Grenot, 1974; Van Devender, 1977; Mares, 1979).

Deserts pose several challenges to small mammals. The suite of adaptive strategies employed in response to heat, aridity, and low vegetative cover is becoming increasingly well understood (Schmidt-Nielsen, 1967; MacMillen, 1972; Mares, 1973), and illustrates the process of convergent evolution (that is, the channeling of adaptations among distantly-related organisms by similar selective pressures toward a particular set or subset of similar morphological, physiological, or ecological characteristics). Nevertheless, in some major desert areas small mammal inhabitants seem to be acquiring adaptations for desert life, but they have not yet reached the pronounced levels of xeric adaptation exhibited by counterparts living in other deserts. I will use the colonization of Australia and South America by rodents to illustrate this point.

Australia originally was a part of the southern section of Pangaea (Gondwanaland) and was largely tropical in climate. As Gondwanaland broke up in the Cretaceous, Australia was connected to Antarctica and shared faunal elements with that continent (Raven and Axelrod, 1972). Gradually the movement of the Australian plate carried the Australian land mass into its current position located between 11° and 38° South Latitude and 112° and 153° East Longitude. This position places it over the 30° Latitude high pressure area where descending, adiabatically-warmed air currents form subtropical deserts (Logan, 1968). The only mammals present on the continent during its earliest formation were monotremes and marsupials; because monotremes were primitive mesic species (Keast, 1972b), the first mammal species to adapt to the newly developing arid area on the mountainless continent were marsupials. In the Pliocene, the Australian continent was colonized across water barriers from southeast Asia by placental murid rodents which subsequently underwent a great adaptive radiation resulting in a diverse array of ecological types (which today includes 13 genera and over 60 species). Among these are members of five genera (*Leggadina, Notomys, Pseudomys, Leporillus, Gyomys*) which are components of the desert fauna (Morton, 1979). Since the colonization route for these island-hopping rodents was via tropical Asiatic islands (Simpson, 1961), they could only begin adapting to the extensive Australian desert in the late Pliocene. Although several genera of rodents have adapted to the Australian desert, species diversity and population density at any particular locality in the desert tends to be low (Watts, 1974; Morton, 1979). Among those species which have adapted to the desert, however, the most conspicuous adaptations are specializations in water conservation (production of an extremely concentrated urine) and locomotion (bipedality) in species of the genus *Notomys* (Walker, 1964; MacMillen and Lee, 1967, 1969; MacMillen et al., 1972; Purohit, 1974). Since marsupials have had a longer period to adapt to the Australian desert, it might be expected that they would also exhibit specializations for life in an arid region, and, indeed, such species as *Dasycercus cristicauda, Sminthopsis crassicaudata, S. froggatti,* and *Setonix brachyurus* are often common desert animals and possess appropriate physiological and anatomical adaptations (Bartholomew, 1956; Bentley, 1960; Schmidt-Nielsen and Newsome, 1962; Walker, 1964; Crowcroft and Godfrey, 1968; Godfrey, 1968; Dawson and Brown, 1970; Purohit, 1971, 1976; Tyndale-Biscoe, 1973).

In South America, the situation is more complex. South America and Africa were originally part of the southern supercontinent and they separated from one another in the early Cretaceous (Dietz and
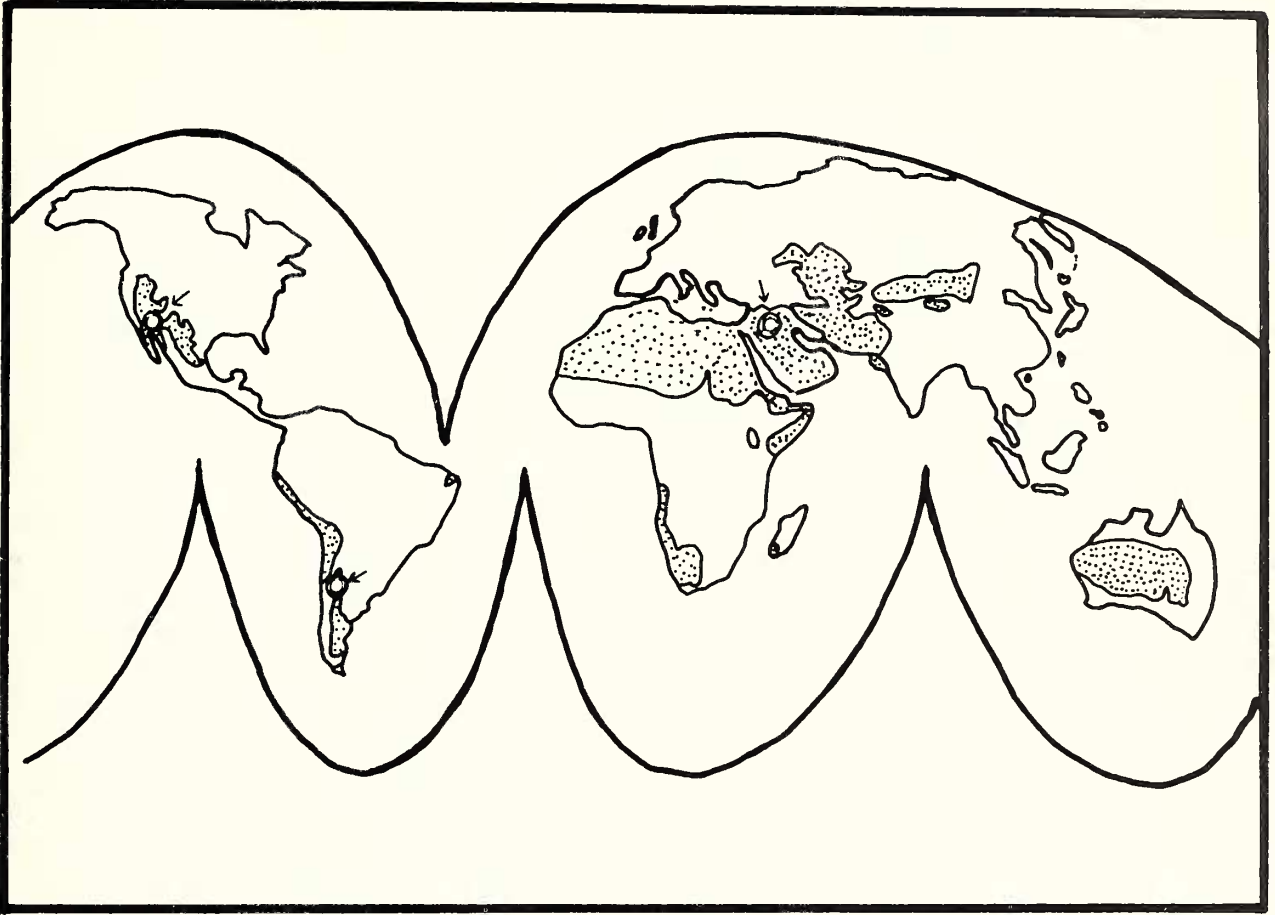
Fig. 1.—The deserts of the world (after Meigs, 1957). The three intensive study sites in the Monte Desert of Argentina, the Sonoran Desert of Arizona, and the Dasht-e-Kavir Desert of Iran are indicated by white dots and arrows.

Holden, 1970) as South America became a huge island which drifted slowly northward and westward. Possibly some of the early mammals (marsupials, edentates, various ancient ungulates) were present on the continent when it broke off of the larger land mass, but subsequent mammalian evolution in South America proceeded in isolation from the rest of the world. In the latest Eocene or early Oligocene a group of caviomorph rodents appeared on the continent. These rodents may have come from either North American stock (Simpson, 1950; Wood and Patterson, 1970; Patterson and Pascual, 1972) or from apparently closely-related African phiomorph rodents (Lavocat, 1969; Hoffstetter and Lavocat, 1970; Hershkovitz, 1972). At about the same time, platyrrhine primates colonized over water from North America. Bats were probably present at this time, and procyonid carnivores appeared in the Miocene (Savage, 1951; Patterson and

Pascual, 1972). No other mammal groups entered the continent until after the completion of the Central American land bridge in the later Pliocene. At that time there was a great influx of diverse mammal types (seven orders, 16 families), which gradually began moving southward on the continent.

Since deserts first formed on the South American continent in the Miocene-Pliocene period, the earliest species to adapt to these arid areas were the caviomorph rodents and the marsupials. Most notable of the latter group were members of the family Argyrolagidae, a group of bipedal, rodent-like animals which were apparently ecological equivalents of present-day jerboas or kangaroo rats. These species were found in southern and northwestern Argentina in areas that are today desert, xeric scrub, and grassland (Simpson, 1970). The recent immigrants to South America probably only encountered the extensive Monte Desert of Argentina

in the latest Pliocene or early Pleistocene, at a time when climatic events were greatly altering the extent and distribution of arid habitats (Mares, 1975a, 1976; Solbrig, 1976). There is good evidence that the deserts of South America were colonized in two major waves from North America, particularly since close fossil relatives of extant South American species have been found in Arizona (Baskin, 1978). The studies of Mares (1975a, 1975b, 1976, 1977a, 1977b, 1977c, 1977d), Mares et al. (1977), Mares and Rosenzweig (1978), and Williams and Mares (1978) have all indicated that the Monte Desert supports a depauperate rodent fauna; that Monte rodents are not highly specialized for desert life; that the most conspicuous faunal elements in the Monte are caviomorph rodents, members of the first wave of colonists to the continent; and that the more recent colonists, muroid (cricetine) rodents, have not evolved specialized desert species, perhaps because there has not been enough time over which such adaptations could have taken place. Most cricetines which inhabit the Monte today either live in patches of more mesic habitat within a larger arid region, or are widespread throughout the thorn scrub or dry montane habitats (for example, puna) which border the desert. Many of their adaptations to aridity (for example, ability to exist with little free water, ability to utilize salt solutions to obtain water, etc., Mares, 1977a, 1977b, 1977c, 1977d) could have evolved as responses to aridity in the high Andean deserts as the animals colonized the continent, and thus functioned as pre-adaptations for life in the lowland Monte Desert when they finally reached the southern third of the continent. The only endemic non-caviomorph rodent in the Monte, *Andalgalomys olrogi*, is closely related to a Paraguayan species and appears to be a relict from a previously widespread Chacoan ancestor (Williams and Mares, 1978).

Recently Marshall (1979), using data in Marshall et al. (1979), Marshall and Hecht (1978), and Reig (1979a, 1979b) has suggested that cricetine rodents may have entered South America as early as 7 Myr BP, or at approximately the same time as the procyonids crossed the water barrier of the Bolivar Trough. This suggestion corresponds roughly to those of Hershkovitz (1966, 1972), and, while unsupported by fossil evidence in northern South America, is based on the appearance of modern cricetine rodent genera in fossil beds of the Montehermosa Fauna of southern Buenos Aires Province, dated at about 3.5 Myr BP (Reig and Linares, 1969).

The neighboring Chapadmalal Fauna contained an even greater number of modern genera and was dated at about 2.7 Myr BP; the latter date corresponds to the suggested time period for the completion of the Panama Land Bridge (see Marshall et al., 1979). Marshall logically reasons that it is unlikely that this rather high diversity of pastorally-specialized rodent species could have developed from what were probably sylvan ancestors, although Baskin (1978) has given strong evidence that at least some South American cricetines (*Calomys*, a generalized genus suggested by Hershkovitz, 1962, to be ancestral to some of the phyllotine rodents) evolved in North America. If cricetines were able to enter the South American land mass as early as suggested, some mechanism to delay their appearance in fossil beds of southern South America by about 3.5 Myr is needed. Marshall proposes that Savanna-grassland habitats did not allow a natural colonization route for northern South American species to reach southern South America until the combined activities of orogenic and glacial events disrupted the major macrohabitats of the continent such that dry habitats became contiguous north and south of the Amazon; since the earliest fossils are already specialized for such habitats, it is suggested that such specialization took place in northern South America (for example, Venezuela, see Sarmiento, 1976). Support for Marshall's ideas concerning habitats are available from various lines of evidence (for example, Mercer, 1973, 1976; Van der Hammen, 1974; Simpson, 1975; Webb, 1978). While this view is markedly opposed to that of Simpson (1951) or Patterson and Pascual (1972), it is still unlikely that colonization of the Monte by cricetine rodents took place much before the Pliocene-Pleistocene interface; no fossil cricetines are known from beds located in areas corresponding to either present-day or suggested Plio-Pleistocene Monte Desert limits.

Mares (1975a, 1976, 1979), Mares and Hulse (1977), and Mares, Enders et al. (1977) have discussed speciation patterns in the deserts of North America and the Monte Desert of Argentina. Both alpha and beta species richnesses are much greater in the northern deserts, not only for rodents, but for other groups of mammals as well. The overall differences in the speciation patterns (and thus patterns of species richness) between the North and South American desert systems may be due to different effects of Pleistocene glaciation in each area. In North America the Pleistocene probably fractured a large, fairly continuous dry area into a num-
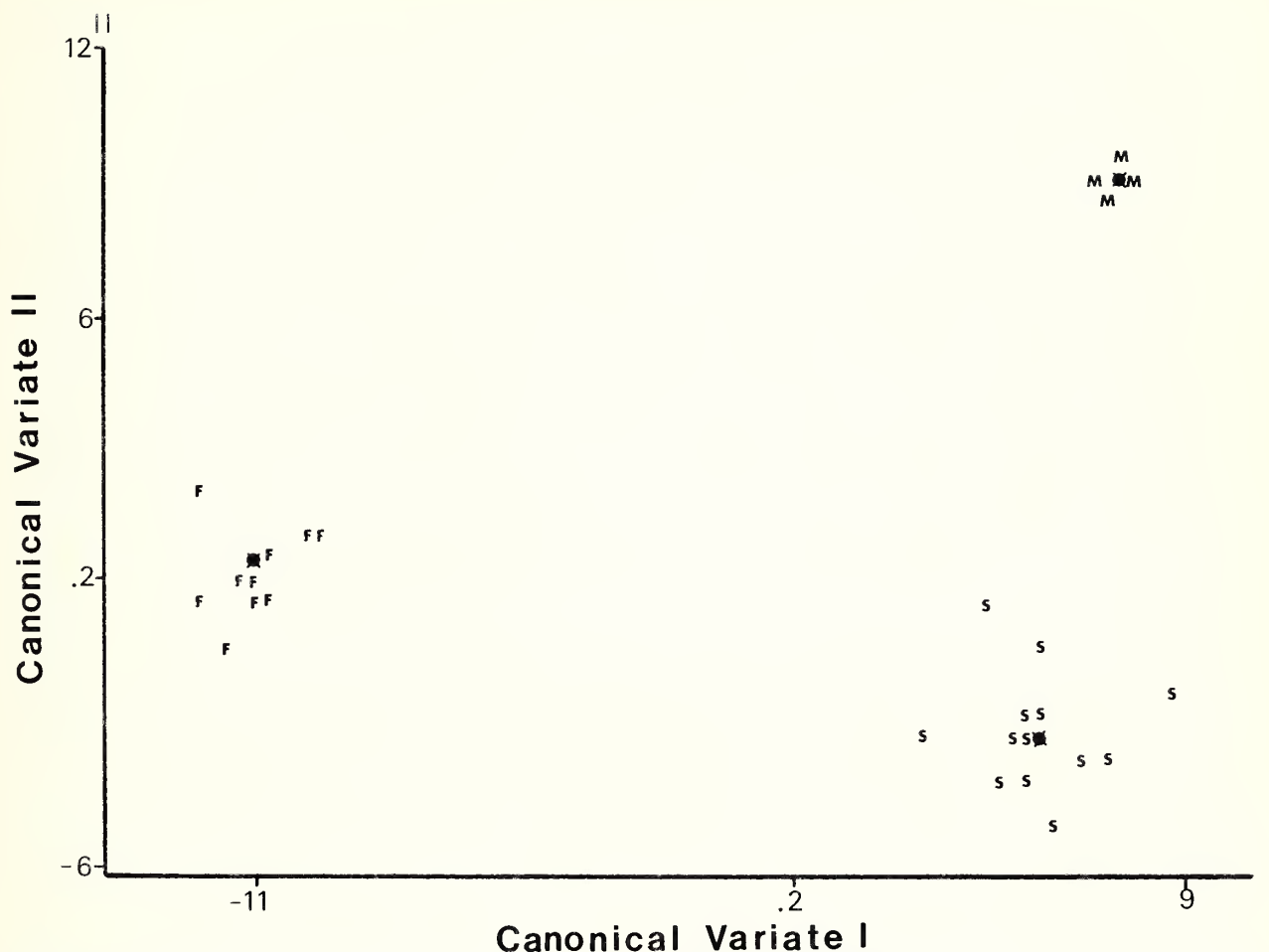
Fig. 2.—A comparison of two desert rodent faunas (Monte and Sonoran sites) and a non-desert coniferous forest rodent fauna from New Mexico utilizing a canonical analysis based on 28 morphoecological traits. The first two canonical variates account for essentially all of the variance in dispersion. The two desert faunas, being plotted closely together on the first axis, are more similar to one another than either is to the forest fauna, even though the latter is closely related, phylogenetically, to the Sonoran assemblage (after Mares, 1973). Individual mean species values are shown by a letter symbol, whereas the faunal mean is given by the large circle.

ber of xeric refugia, thus forming a system conducive to species multiplication via geographic isolation, whereas in the Monte Desert, the Pleistocene may have isolated the desert ecosystem into a single, relatively small refugium in which some species (including, perhaps, the argyrologid marsupials) went extinct (Mares, 1979). A system whereby a single refugium formed repeatedly would function as an extinction system leading to reduced species diversity because of the island nature of such a desert preserve (see MacArthur and Wilson, 1967; Diamond and May, 1976), while a system of multiple desert refugia, such as what probably obtained in North America during the Pleistocene, would act as a species multiplication system (Mares, 1979).

Obviously, the rodents of the North and South American desert systems were quite distinct, phylogenetically, from each other as well as from those species which were entering Australia at about the same time. Yet each group of rodents encountered elevated temperatures, great insolation, low and sporadic precipitation, and low productivity. Other rodents were encountering similarly harsh environments during their independent evolution in Africa and Asia.

Mares (1976) compared morphological and ecological aspects of a locality in the Monte Desert (near Andalgalá, Catamarca Province, Argentina) with one from a site in the Sonoran Desert (near Tucson, Arizona, USA). The Sonoran Desert is quite similar floristically, climatologically, and geo-

morphologically to the Monte Desert (Orians and Solbrig, 1977), although its rodent fauna has been associated with developing arid, semiarid and grassland communities since at least the Oligocene (Wood, 1935; Lidicker, 1960; Voorhies, 1975), and thus they have had more time to adapt to aridity. Mares also compared the rodent fauna of a non-desert community (a Western Yellow Pine area in central New Mexico, USA) with the two desert faunas to determine if the latter were more similar to each other morphologically than were the two North American faunas. Phylogenetically, the two northern faunas were more closely related than were those of the North and South American deserts. By subjecting numerous morphological characteristics, which were selected because they presumably reflected ecological functions, to several multivariate mathematical techniques (principal components analysis, cluster analysis, discriminant function analysis, and canonical analysis), Mares was able to show that the rodents from the two desert areas were more similar to one another, despite the fact that they were more distantly related, than were the two North American faunas (Fig. 2). Convergent evolution had occurred between the desert rodents and similarities were particularly apparent in several traits associated with a desert existence (for example, various dental characteristics, inflated tympanic bullae, light-colored pelage, and others). These similarities might have been even greater had the historical biogeographic histories of the two deserts been more comparable.

In these earlier papers (Mares, 1975b, 1976), I attempted to assess the degree of convergent evolution existing between two disjunct desert rodent faunas as indicated by the mathematical techniques. Before I utilized morphological measurements in the comparative analyses, however, I spent much time and effort studying the distribution, natural history, reproductive biology, physiology, and population ecology of many of the Monte Desert species; Sonoran Desert rodents had been well-studied by others for more than a half-century. My familiarity with many aspects of the biology of the Argentine species allowed me to arrive at a rough determination of the degree of difference or similarity between the two amphitropical desert faunas. This determination was subjective in the sense that any ecologist who had spent a number of years working with the mammals of the Monte, and who possessed familiarity with the northern species, would very likely have developed some opinions

regarding which species might fill similar niches in each area. Although some proposed examples of convergent pairs were obvious (for example, *Ctenomys* and *Dolichotis* of the Monte versus *Thomomys* and *Lepus* of Arizona), other suggested equivalents might have found less acceptance among investigators (for example, *Octomys* and *Microcavia* of the Monte versus *Neotoma* and ground-dwelling sciurids of Arizona). Thus the problem I faced was to encounter some method of objectively comparing at least portions of the niche space of each species, that is, its ecological position within each desert.

Form and function have long been known to be associated (for example, Darwin, 1859, discussing Galápagos Island finches; Thompson, 1917). An organism's morphology is the product of synergistic interactions of its environment and its genetic makeup, but various functional attributes can generally be deduced from disparate morphological traits. Many investigators (for example, Shoener, 1965; Tamsitt, 1967; Cody, 1975; Karr and James, 1975; Findley, 1976) have pointed out that numerous ecological characteristics of organisms are strongly correlated with morphological traits (see also Hespenheide, 1973). I found that by analyzing a number of morphological traits I was able to arrive at a statistical comparison between rodents of both deserts that seemed logical from the ecological point of view. Some of these traits, such as the long hind legs and tail of desert rodents which are associated with bipedal locomotion, readily suggest a function; others, such as the width across the zygomata have a less obvious functional relationship. In quantifying these traits, and comparing them between faunas, I distinguished between these two types of morphological measurements (Appendix 1). In fact, both sets of measurements gave a reasonable interpretation of similarities between distantly-related species, but it is sometimes easier to see the functional applicability of one or more traits, because they strongly reflect ecological function. To use an extreme example, it would be quite surprising to find an herbivorous felid possessing the shearing teeth of a carnivore; the basis for assigning function to form is well-grounded in comparative zoology. Thus, I assigned an ecological function to diverse morphological traits and termed these traits "morphoecological" characteristics (Mares, 1975b); the subordinate position of the prefix *eco* to *morpho* is intentional and points out that the traits are, above all, morphological and may be quite labile in their

Fig. 3.—A site in the North American desert near Needles, California, where low shrubs (especially creosotebush, *Larrea tridentata*) and bursage (*Franseria*) predominate.

ecological implementation. Nevertheless, I feel that it is possible to arrive at a first approximation of locomotor, trophic, physiological, and habitat similarities using nothing more than these types of measurements. Also, since most desert rodents of the world are poorly studied ecologically, such analyses should yield an impression of the ecological mosaic formed by the various rodent species comprising a particular fauna, as well as an indication of the evolutionary forces that seem to mould fairly predictable sets of species in widely scattered xeric regions.

The limitations of this method are obvious. If we begin with a well-studied fauna, such as the rodents of the Sonoran Desert of Arizona, and compare these with species which are essentially ecologically unknown, then we arrive at a comparison of morphoecometrics of the two groups. The underlying assumption is that a member of the unknown fauna sharing many functional traits with a species in the well-studied group probably fills a similar role in its own ecosystem. Thus a species in the Monte Desert, such as *Eligmodontia typus*, might be closely allied morphoecologically with *Peromyscus eremicus* of Arizona, meaning that such traits as overall body size and dimensions, ear length, omnivorous food habits, scansorial locomotion, pelage color

and auditory bullae size, are shared between the species. *E. typus* differs in having longer hind feet and a longer tail, which reflects its propensity to inhabit fairly open sandy habitats. In this respect it is more similar to members of the genus *Perognathus*, and this fact can be inferred from the analyses. Such traits of *Eligmodontia* such as its ability to extract water from cacti or to process solutions of extreme salinity (Mares, 1975a, 1977a) are not apparent from the measurements analyzed. Thus, regardless of the degree of sophistication of a morphological study, many important attributes of a species will only be discovered through intensive field and laboratory investigations.

Up to now comparative multivariate morphometrics have been limited to analyses within higher taxa (Chiroptera, Rodentia, small birds, etc.) because of the difficulty in utilizing sets of measurements across morphologically unlike groups. Hence such important competition studies of widely differing taxa, such as those concerning the interactions of granivorous desert ants and mammals (Brown and Davidson, 1977), do not lend themselves to these methods. However, the multivariate Monte-Sonoran desert rodent comparison did suggest that granivory was an important attribute of rodents of Arizona and unimportant among those of the Monte.

Fig. 4.—A view of the Campo Arenal in the Monte Desert of Catamarca Province, Argentina, with *Larrea cuneifolia* as the dominant.

These observations led directly to a comparison of the patterns of granivory of birds, ants, and rodents in the two deserts (Mares and Rosenzweig, 1978).

With the limitations of these techniques in mind (Appendix 2), and with a belief that a first comparison of the ecological aspects of the desert rodent faunas of the world is at least desirable, I will proceed to an analysis of morphoecological traits of the numerous species of rodents which have managed to successfully inhabit one of the earth's most challenging regions.

A THREE-DESERT COMPARISON OF CONVERGENT EVOLUTION

The rodent faunas of the Sonoran and Monte deserts were not as similar as might have been expected given the great similarities in their environments. If the lack of more pronounced convergent evolution is a result of a time factor (perhaps because the Monte rodents have not had sufficient time to specialize for desert life because of their late arrival to the Monte), then one can presumably test this hypothesis by comparing both deserts with a third, environmentally-similar area with an evolutionary history more like that of the North American desert. In the following example, the third desert area chosen was the Dasht-e-Kavir of Iran.

The Iranian Desert has a winter-rain Mediterranean climate much like the Great Basin Desert of North America, and not like the bimodal, summer-winter precipitation characteristic of the northern Sonoran Desert, or the summer rainfall of the northern Monte (Ganji, 1955; Jaeger, 1957; Morello, 1958). Basically, however, all three areas are warm, subtropical deserts. All have a basin and range topography, with the two northern deserts being most similar in this regard (Zohary, 1963; Lustig, 1968; Logan, 1968). The two New World deserts have a pronounced tree and tall-cactus component, while the Kavir is a low shrub desert, but extensive areas of physiognomically similar habitats can be found in all three deserts (Figs. 3–5).

The rodents of the Dasht-e-Kavir have had a long history of association with arid areas, either in Iran proper or in more northern Old World deserts, and they are phylogenetically less closely related to the rodent faunas of the two New World deserts than the latter are to each other (Simpson, 1945; Ellerman, 1949; Hall and Kelson, 1959; Dawson, 1967). Thus any similarities between the rodent faunas of the two deserts which have had a similar period of time for desert adaptations to develop would have to override those characteristics which might be due to common inheritance of the Sonoran and Monte desert rodents (that is, parallelism).

Fig. 5.—A locality in the Dasht-e-Kavir Desert of Iran about 100 km southeast of Tehran, chenopodeaceous shrubs predominating.

Methods

The basic statistical techniques utilized in the following analyses are stepwise discriminant function analysis, canonical analysis, and cluster analysis. The first technique is a fairly straightforward method of comparing the ability of a number of variables to distinguish between groups that have been previously delineated. Thus, if variable a is some morphological measurement that best distinguishes between the groups, and variable b is a separate variable, uncorrelated with a, and that is the second best variable to distinguish between the groups, then these two variables are weighted and combined to form a linear discriminant function. The number of discriminant functions formed may be one less than the number of groups, or may be equal to the number of variables, depending on the significance with which the groups are distinguished. After the discriminant functions are formed, the groups are classified and the individual members comprising each group are compared to the overall group variables to assess the statistical validity of their inclusion within a particular group. This allows for a determination of the precision of group assignations, as well as a method of calculating the probability that a group member actually belongs in another of the assigned groups rather than in the group under consideration.

The second technique, canonical analysis, proceeds from the first. Here, the original variables are used to form a separate set of canonical variables which are themselves uncorrelated with one another. The members of each group are then plotted along each canonical axis (often the first two axes explain the greatest amount of variance in the data), and the distances in n-dimensional space (Mahalanobis distance), where n = the number of variables, are given for each group member to its group mean value, and to every other individual being examined. It is thus possible to get a 2-dimensional visual impression of n-dimensional spatial relationships. For example, if there is great overlap between groups with many of their component members being similar to others in separate groups, the plot would indicate approximately the same space being occupied by all groups. Similarly, if only one or two group members are generally similar to those of another group, the former may be plotted more closely to members of the latter group (see also Heyck and Klecka, 1973; Klecka, 1975; Cody, 1978). Cluster analysis has been widely discussed in the literature and will not be explained here (for example, Cooley and Lohnes, 1971; Sneath and Sokal, 1973).

The species analyzed in the three-desert comparison are listed in Table 1, while Table 2 lists the morphoecological traits utilized in the analyses. The rationale for measurements is discussed at length in Appendix 1. In addition to the rodents used in the earlier North American-South American comparison, representatives of rodent species from a locality located approximately 100 kilometers southeast of Tehran, Iran, were included in the present analysis. Individuals were measured and the data were subjected to various multivariate techniques including stepwise discriminant function analysis and canonical variate analysis (BMDP and SPSS programs), and the cluster analysis techniques of the NT-SYS computer program package of F. James Rohlf of the State University of New York at Stony Brook. The unweighted arithmetic pair-group method with averages was used to generate phenograms, and both distance and correlation phenograms were plotted.

I separated the North and South American rodent assemblages into a number of loose functional groups. These included the following categories: *Dipodomys* (the bipedal heteromyids); *Perognathus* (the quadrupedal heteromyids); Sonoran (the remainder of the Arizona rodents); "gophers" (the highly fossorial *Thomomys* of Arizona and *Ctenomys* of Argentina); and Monte (all Monte rodents excepting *Ctenomys*). Each rodent species from the Iranian Desert was entered into the multivariate analysis as

Table 1.—*Rodent species in one locality each of the Monte Desert of South America, the Sonoran Desert of North America, and the Dasht-e-Kavir Desert of Iran.*

Sonoran (Tucson)	Monte (Andalgalá)	Iran (near Tehran)
Family Heteromyidae	Family Cricetidae	Family Cricetidae
Perognathus baileyi	Subfamily Cricetinae	Subfamily Cricetinae
Perognathus intermedius	Tribe Hesperomyinae	Tribe Cricetini
Perognathus penicillatus	*Eligmodontia typus*	*Calomyscus bailwardi*
Perognathus flavus	*Phyllotis griseoflavus*	Subfamily Gerbillinae
Dipodomys merriami	Family Caviidae	*Meriones libycus*
Dipodomys spectabilis	*Microcavia australis*	*Meriones crassus*
Dipodomys ordii	Family Octodontidae	*Meriones persicus*
Family Geomyidae	*Octomys mimax*	*Gerbillus nanus*
Thomomys bottae	Family Ctenomyidae	Family Dipodidae
Family Cricetidae	*Ctenomys fulvus*	*Allactaga elater*
Subfamily Cricetinae		*Jaculus blandfordi*
Tribe Hesperomyinae		
Neotoma albigula		
Peromyscus eremicus		
Peromyscus maniculatus		
Onychomys torridus		
Reithrodontomys megalotis		
Reithrodontomys fulvescens		
Sigmodon hispidus		
Family Sciuridae		
Ammospermophilus harrisi		

being of "unknown affinity", and the computer procedure was to assign each unknown to one of the previously described major groups, the assignation being based on the number and interrelationships of shared character states.

Results and Discussion

The rodent fauna of the Kavir site is not nearly as rich in species as is the Tucson site, rather it resembles that of the Andalgalá locality in the Monte Desert (Table 1, Figs. 14–16). Rodents seem to be abundant in the Kavir, however (Lay, 1967; Mares, personal observation), and the low densities of rodents and other small mammals in the South American desert is an uncommon observation for a major desert area; this is also the case in Australia (for example, Schall and Pianka, 1978; Morton, 1979). Possibly the fact that Monte rodents are less specialized for desert life helps account for the differences in relative abundances evident among the three deserts, although the Pleistocene history of extinction and the coevolutionary relationships of plants, ants, and granivorous rodents might also be an important factor in the smaller population sizes of rodents supported in the Argentine desert (Mares and Rosenzweig, 1978; Mares, 1979; Morton, 1979).

The positioning of members of the Iranian, Sonoran, and Monte rodent faunas on the first two canonical axes when only external traits were utilized is shown in Fig. 6, while Table 3 gives the loadings of each variable making up the first two canonical variates. The expectation that the similarities between Iran and Sonora would override the phylogenetic relationships of the Sonoran and Monte deserts was not entirely realized. The Sonoran and Monte rodents are closer to one another than either is to the Iranian fauna. The mean Mahalanobis Distance (D^2) of the Sonoran bipedal *Dipodomys* species to the Iranian species is 9.8 units, while the mean distance of each Sonoran species to its faunal mean is 18.5 units. The distance of the Sonoran bipeds to the Monte is 14 units. In fact, two Sonoran species, the bannertail kangaroo rat, *Dipodomys spectabilis,* and the grasshopper mouse, *Onychomys torridus,* were assigned to the Iranian desert. Two other species, the white-throated woodrat, *Neotoma albigula,* and the gopher, *Thomomys bottae,* were placed with the Monte rodents. The assignments were undoubtedly based on the Iranian desert having few species, but two of these are bipedal forms (like *Dipodomys*) and one is a cricetine with coronally-hypsodont dentition

Table 2.—*Morphological measurements, ratios, and categories used in the various multivariate determinations. Measurements denoted by an asterisk (*) are traits which reflect ecological aspects quite strongly (Figs. 21, 23). Those marked with a (¹) were used in the analyses given in Figs. 6, 10; those with a (²) were used in computing Figs. 7, 11, 19; those with a (³) were utilized in Figs. 20, 24 whereas all traits (except weight) were used in Figs. 18, 22.*

External	Cranial
1) Head-body length (HBL)[1,3]	15) Basal length (BL)[2,3]
2) Tail length (TL)[1,3]	16) Incisor-molar length (IML)[3]
3) Hind foot length (HFL)[1,3]	17) Bullar length (UL)[3]
4) Height of ear from notch (EL)[1,3]	18) Bullar width (UW)[3]
5) Length of longest vibrissae (VL)[1,3]	19) Width across molariform tooth rows (mouth width) (MW)[2,3]
6) Length of hair between shoulders (HL)[1,3]	20) Zygomatic breadth (ZB)[3]
*7) Tail length/head-body length (TL/HBL)[1]	21) Incisor width (IW)[2,3]
*8) Hind foot length/head-body length (HFL/HBL)[1]	22) Incisor length (IL)[2,3]
*9) Ear length/head-body length (EL/HBL)[1]	*23) Incisor-molar length/basal length × 100 (IML/BL)[2]
*10) Vibrissae length/head-body length (VL/HBL)[1]	*24) Bullar index (UI)[1]
*11) Hair length/head-body length (HL/HBL)[1]	25) Length of molar tooth row (TRL)[2,3]
*12) Weight (W)[1]	*26) Tooth row length/incisor-molar length × 100 (TRL/IML)[2]
*13) Foot bristles (FB)[1,3]	*27) Width across tooth rows/basal length × 100 (TRL/BL)[2]
*14) Tuftiness of tail (TT)[1,3]	*28) Zygomatic breadth/basal length × 100 (ZB/BL)
*41) Vibrissae density (VD)[1,3]	*29) Incisor width/basal length × 100 (IW/BL)[2]
	*30) Incisor length/basal length × 100 (IL/BL)[2]
	*31) Incisor angle (IA)[2,3]
	*32) Seizer-digger incisors (SZ)[2,3]
	*33) Triturator incisors (TI)[2,3]
	*34) Molar planation (MP)[2,3]
	*35) Molar complexity (MC)[2,3]
	*36) Tubercular hypsodonty (TH)[2,3]
	*37) Coronal hypsodonty (CH)[2,3]
	*38) Molar triangulation (MT)[2,3]
	39) Molar tooth row width (TW)[2,3]
	*40) Relative molariform surface area (SA)[2]

(like *Onychomys*). The Monte, with even fewer species, has a rodent (*Octomys mimax*) which strongly resembles a woodrat, externally, and a fossorial tuco-tuco (*Ctenomys*) which is practically indistinguishable from a North American geomyid.

The location of the three desert faunas plotted on the first two canonical axes when only dental traits are utilized is given in Fig. 7; Table 4 shows the weightings of the various characteristics on the canonical variates. As before, the Sonoran and Monte rodents are closer to each other than either is to the Iranian group, while the latter is most similar to the North American desert. This same pattern was obtained using 25 ecological variables.

Correlation and distance phenograms were computed using 25 morphoecological variables (Figs. 8 and 9). In the correlation phenogram (Fig. 8), a number of points are of interest. The first cluster is composed of a large group of North American desert specialists, the heteromyids (pocket mice and kangaroo rats, here termed "K-rats"), which are grouped fairly tightly, and this cluster is loosely linked to one containing the two bipedal dipodids,

Allactaga and *Jaculus*, of the Iranian Desert. No Monte species are included within this large cluster. The second grouping includes most Sonoran Desert small scansorial micro-omnivores ("peromyscines"), as well as the leaf-eared mouse, *Phyllotis (Graomys) griseoflavus*, of the Monte. The carnivorous-insectivorous grasshopper mouse of Arizona, *Onychomys torridus*, is closely clustered with the hamster of Iran, *Calomyscus bail-*

Table 3.—*The coefficients for each of the original variables forming the first two canonical variates in Fig. 6.*

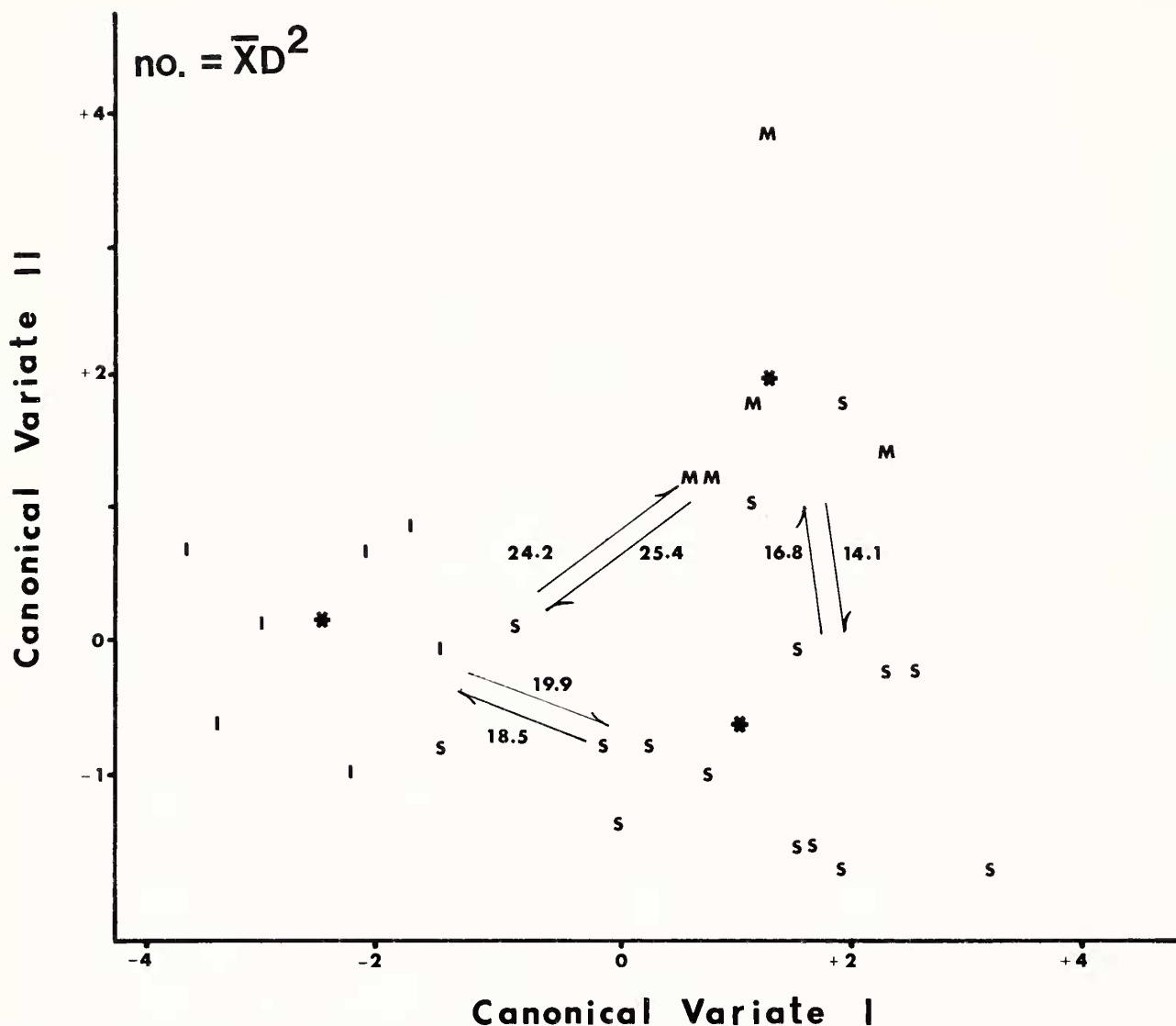| Original variable	Canonical variate 1	Canonical variate 2
TL/HBL	0	0
HFL/HBL	0	−.2
EL/HBL	−.1	.1
VL/HBL	0	0
HL/HBL	−.1	0
W	0	0
FB	0	1.5
TT	−.6	−.3
VD	2.5	.5

Fig. 6.—A canonical analysis of external morphological traits comparing the Monte, Sonoran, and Iranian rodent faunas. Individual species means are shown by the appropriate letter symbol, whereas the faunal mean is denoted by an asterisk (*).

wardi. The next clusters involve Arizona and Argentine species only, with no Iranian species being grouped with (that is, being ecological equivalents of) the "wood rats" (scansorial, medium-sized herbivores), the "ground squirrels" (scansorial, medium-sized omnivores and/or herbivores which burrow extensively), or the "gophers" (highly fossorial root, tuber, and above ground vegetation feeders). The final cluster, loosely joined to the "gopher" group, is comprised of the Iranian jirds, *Meriones*, and the Monte caviomorph, *Octomys mimax*.

The distance phenogram (Fig. 9) presents a somewhat different view of the three desert rodent fau-

nas. Now there is a major cluster of desert rodents made up largely of the heteromyids, the small *Gerbillus nanus* and the *Meriones* species of Iran, and the Monte caviomorph, *O. mimax*. The other clusters are similar to those of the correlation phenogram, except that the bipedal dipodids are only loosely grouped with the rest of the desert rodents. The inclusion of *Octomys* within the category which I have termed "desert specialists" is not surprising considering that this is a highly desert adapted caviomorph which inhabits extremely arid areas within the Monte subsisting largely on cacti and other vegetation and, in other respects as well,
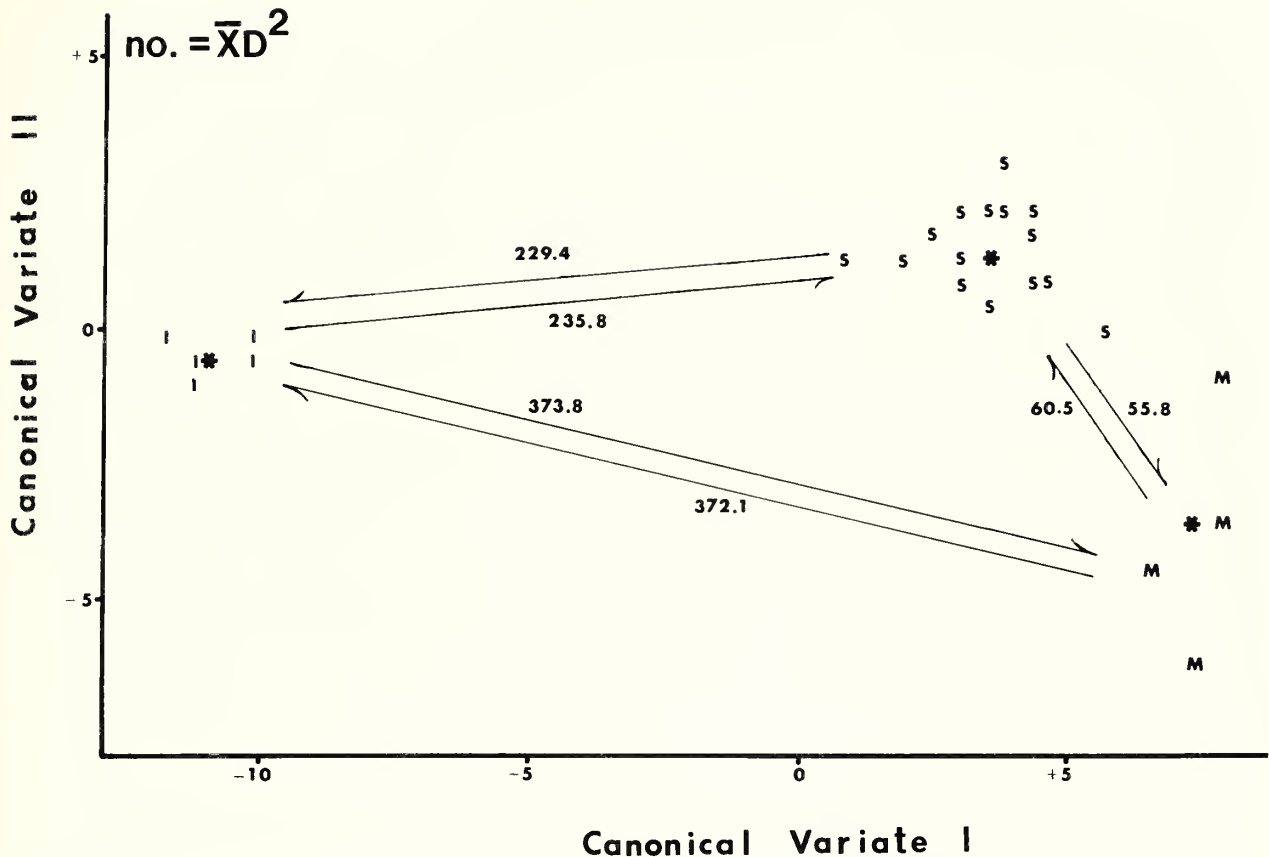
Fig. 7.—A canonical analysis utilizing 23 dental traits in a comparison of three desert rodent faunas. Individual species mean values are denoted by the appropriate letter symbol, whereas the faunal mean is indicated by an asterisk (*).

being similar to the wood rats (*Neotoma*) of North America (Mares, 1976). However, the failure of the dipodids to be clustered, even tenuously, with the heteromyids was not expected. Both of these groups of desert rodents have long been considered ecological equivalents that have strongly converged in their morphology and ecology in becoming highly adapted desert specialists (Howell, 1932; Vaughn, 1972; Gunderson, 1976).

In order to determine why such a priori examples of convergent evolution were not clustered together as ecological equivalents, I performed a series of stepwise discriminant function and canonical analyses on two subsets of the data. In examining the characteristics that were utilized in the cluster analyses, it became apparent that two major ecological parameters were being measured—food habits and food procurement (certain dental and cranial measurements); and locomotion and overall external appearance (most external measurements). When these two groups of traits were analyzed separately

(Table 2), each analysis produced a markedly different pattern.

The canonical analysis based on external characteristics is given in Fig. 10. The Mahalanobis Distance (D^2) values for the group means and for the various unknowns are given in Table 5, while the approximate weightings of each trait forming the canonical variates are shown in Table 6. Both *Allactaga* and *Jaculus* were assigned to the *Dipodomys* group, along with *Gerbillus nanus*. *Callomyscus* and the two jirds, *Meriones crassus* and *M. persicus*, were assigned to the Sonoran assemblage, while the remaining jird, *M. libycus*, was assigned to the "gopher" group. From the loadings on the first two canonical variates, it can be seen that Canonical Variate 1 is composed primarily of variables describing foot bristles, relative ear, hair, and hind foot lengths, and vibrissae density. On Canonical Variate 2, vibrissae density, tail tuftiness, and relative ear and hind foot lengths are weighted fairly heavily. Thus it appears that species located on the
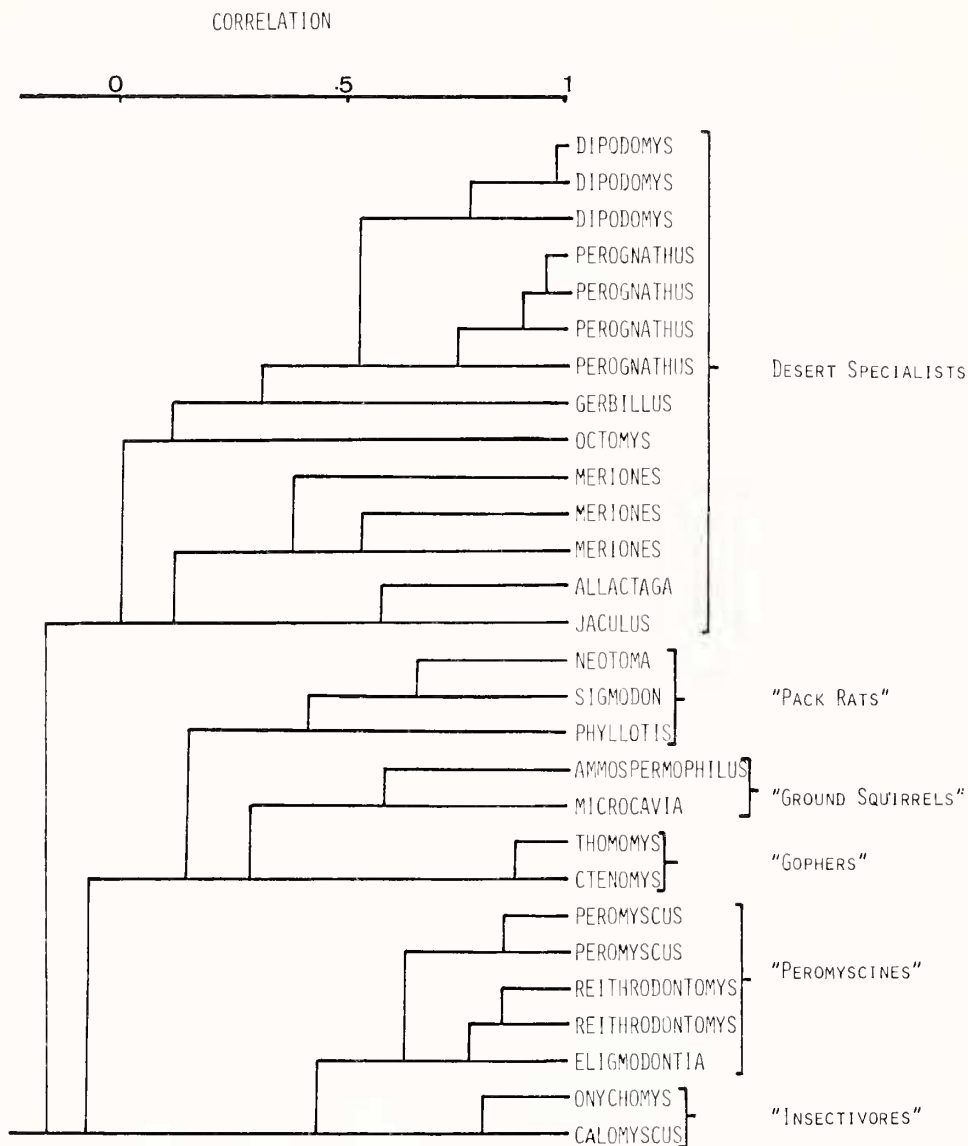
Fig. 8.—A correlation phenogram of the rodents of three deserts based on 25 morphoecological traits. *Allactaga* and *Jaculus*, thought to be Old World equivalents of kangaroo rats (*Dipodomys*), are not clustered with the heteromyids. Most Sonoran and Iranian species fall into the "desert specialist" category.

Table 4.—*The coefficients for each of the original variables forming the first two canonical variates in Fig. 7.*

Original variable	Canonical variate 1	Canonical variate 2
W	−.1	0
IML/BL	.1	−.1
TRL/IML	0	−.2
MW	−.4	.6
ZB/BL	.1	−.1
IW/BL	2.2	1.4
IL/BL	−1.0	−.7
IA	−1.8	−.7
SZ	−6.1	−2.3
MP	1.5	1.0
MC	3.5	−.2
TH	.4	.3
CH	−2.6	.7
MT	2.0	−2.5
SA	31.8	−6.2

left half of the figure would possess dense vibrissae and have fairly long hind feet, while those located in the upper part of the figure would have tails with conspicuous tufts, as well as relatively long hind feet and ears. It is evident from Table 5 that the D^2 distances from the Kavir species to each of the assigned group means were often quite close and final determination of the most similar group was based on small differences in n-dimensional space. *Gerbillus nanus*, for example, was located 54.5 units from the *Dipodomys* mean and only 54.9 units from the Sonora mean value. The slightly greater dis-
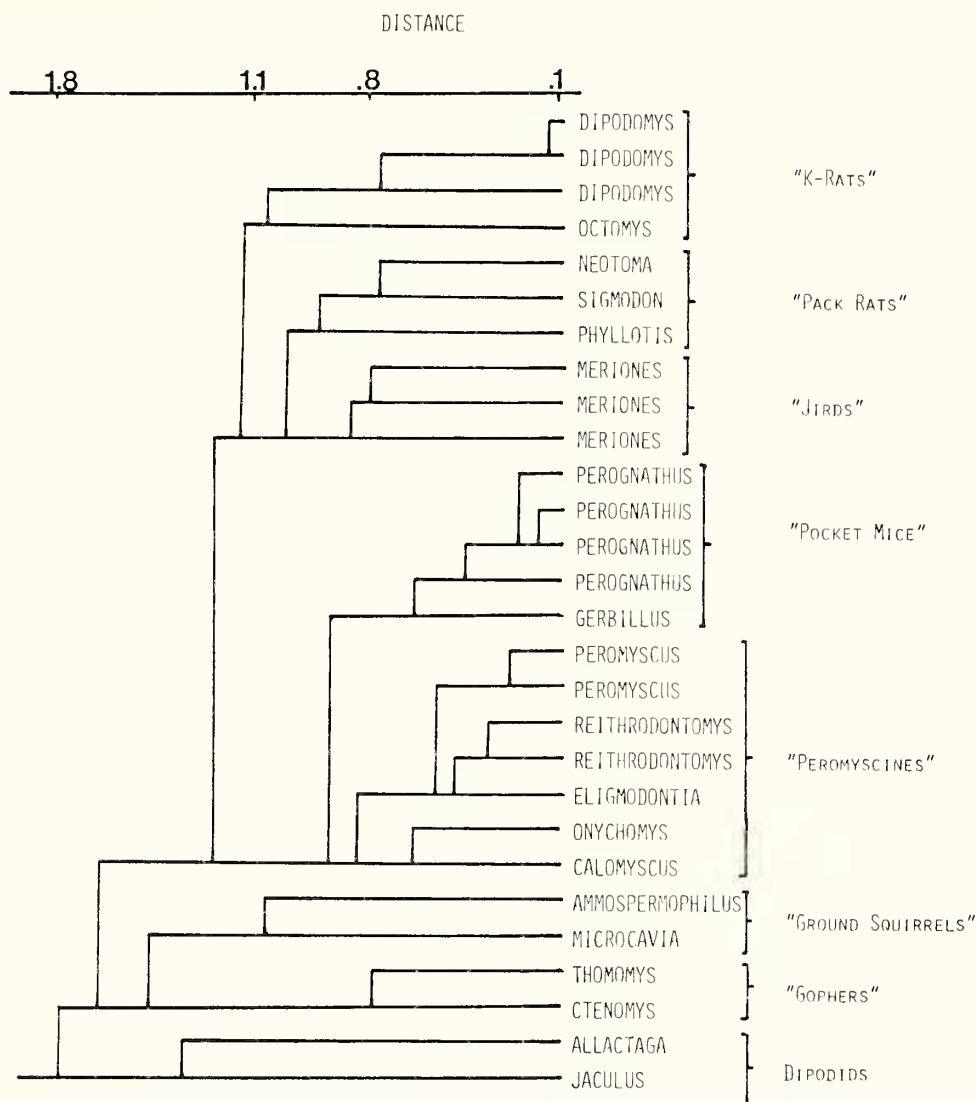
Fig. 9.—A distance phenogram of the rodents of three deserts based on 41 morphological traits. Dipodids are greatly separated from the remainder of the rodents.

Table 5.—*Square of the Mahalanobis Distance (D^2) of each of the groups and unknowns examined in an analysis of external characteristics (Fig. 10). Mean ± SD.*

Group	Mean D^2 values				
	Dipodomys	*Perognathus*	Sonora	"Gophers"	Monte
Dipodomys	4.3 ± 3.0	40.8 ± 23.6	170.9 ± 25.3	335.7 ± 39.2	216.1 ± 18.2
Perognathus	39.5 ± 5.6	3.0 ± 1.2	138.0 ± 20.9	285.7 ± 26.7	216.3 ± 26.7
Sonora	175.6 ± 29.9	144.0 ± 26.6	8.9 ± 3.0	69.4 ± 17.5	37.2 ± 9.0
"Gophers"	335.4 ± 39.5	286.7 ± 32.1	64.4 ± 10.0	3.95 ± 0	84.1 ± 5.4
Monte	221.8 ± 23.7	223.3 ± 36.0	38.2 ± 15.7	89.8 ± 6.9	10.0 ± 1.3
Calomyscus	121.1	146.8	42.6	158.9	60.8
Gerbillus	54.4	62.7	54.9	164.9	107.8
Meriones libycus	323.2	315.1	48.4	42.1	46.8
Meriones crassus	203.7	189.1	17.0	40.9	46.7
Meriones persicus	143.9	147.8	39.1	124.1	78.7
Allactaga	447.5	631.7	628.3	853.6	479.7
Jaculus	131.4	264.5	485.2	691.5	462.2

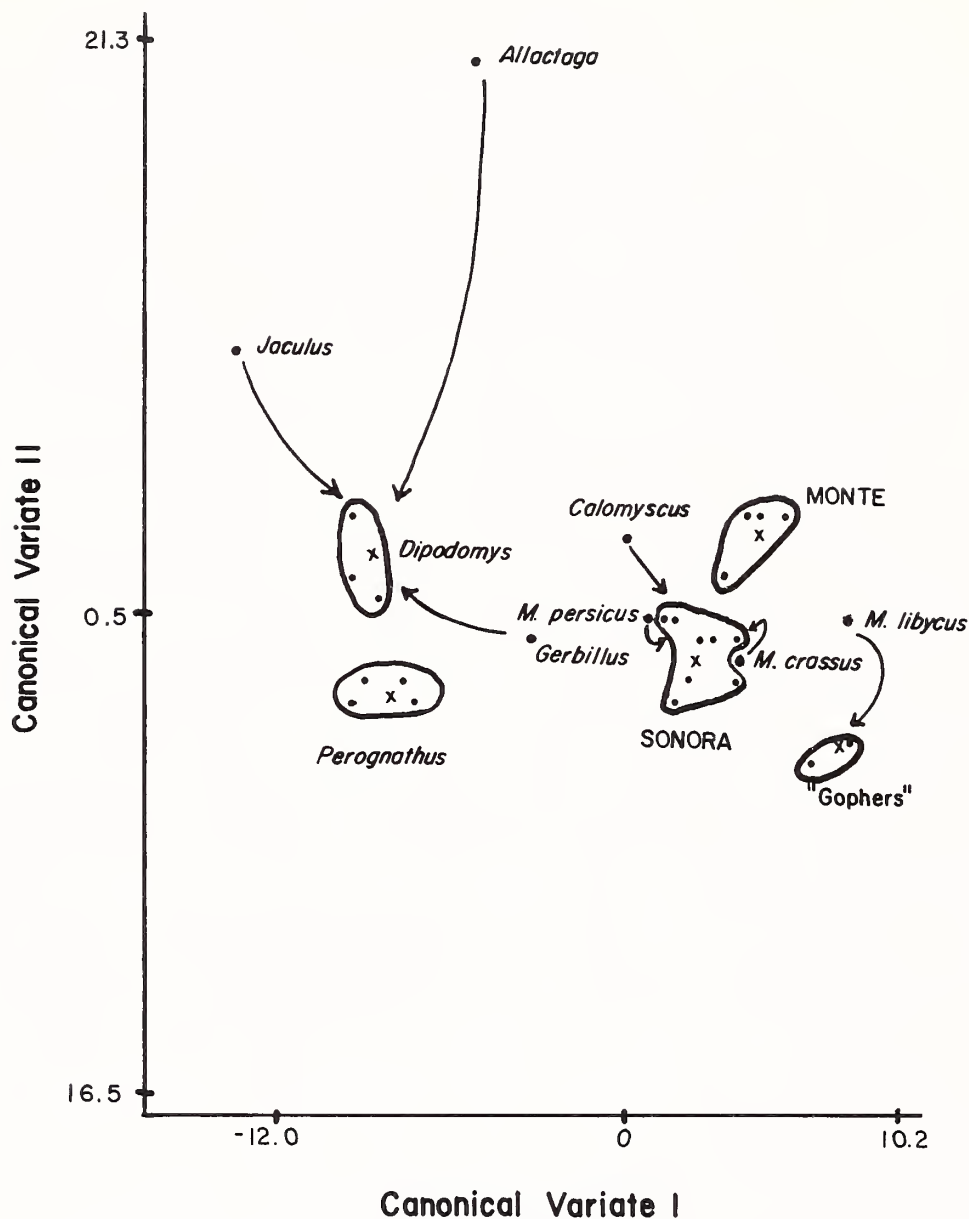Fig. 10.—A canonical analysis of rodents from three desert localities based on external traits. Iranian rodents have been assigned as unknowns, whereas the North American and Monte rodents have been broken into a number of functional groups. Bipedal *Allactaga* is placed with *Dipodomys*; quadrupedal *Meriones* is placed with the "gophers." × equals group means; dots equal cages.

tance from the Sonora mean is almost certainly due to the disparate nature of the species comprising The Sonoran assemblage, including medium-sized ground squirrels (*Ammospermophilus*) and cotton rats (*Sigmodon*), as well as small scansorial cricetines. It should be noted that the distance of *Gerbillus* to the *Perognathus* mean was only 64.4 units. *Allactaga* was over three times farther from the *Dipodomys* mean than was *Jaculus* (447.5 versus 131.4 units, respectively).

In the analysis of dental characteristics (Fig. 11, Tables 7 and 8), the three species of *Meriones* were all assigned to the *Dipodomys* category, with *M. libycus* being the most similar to the *Dipodomys* group. *Gerbillus* and *Calomyscus* were also assigned to the kangaroo rat assemblage. The two dipodids were assigned differently, with *Jaculus* being placed with the kangaroo rats, while *Allactaga* was grouped with the "gophers." The weightings of the various dental characteristics on the first
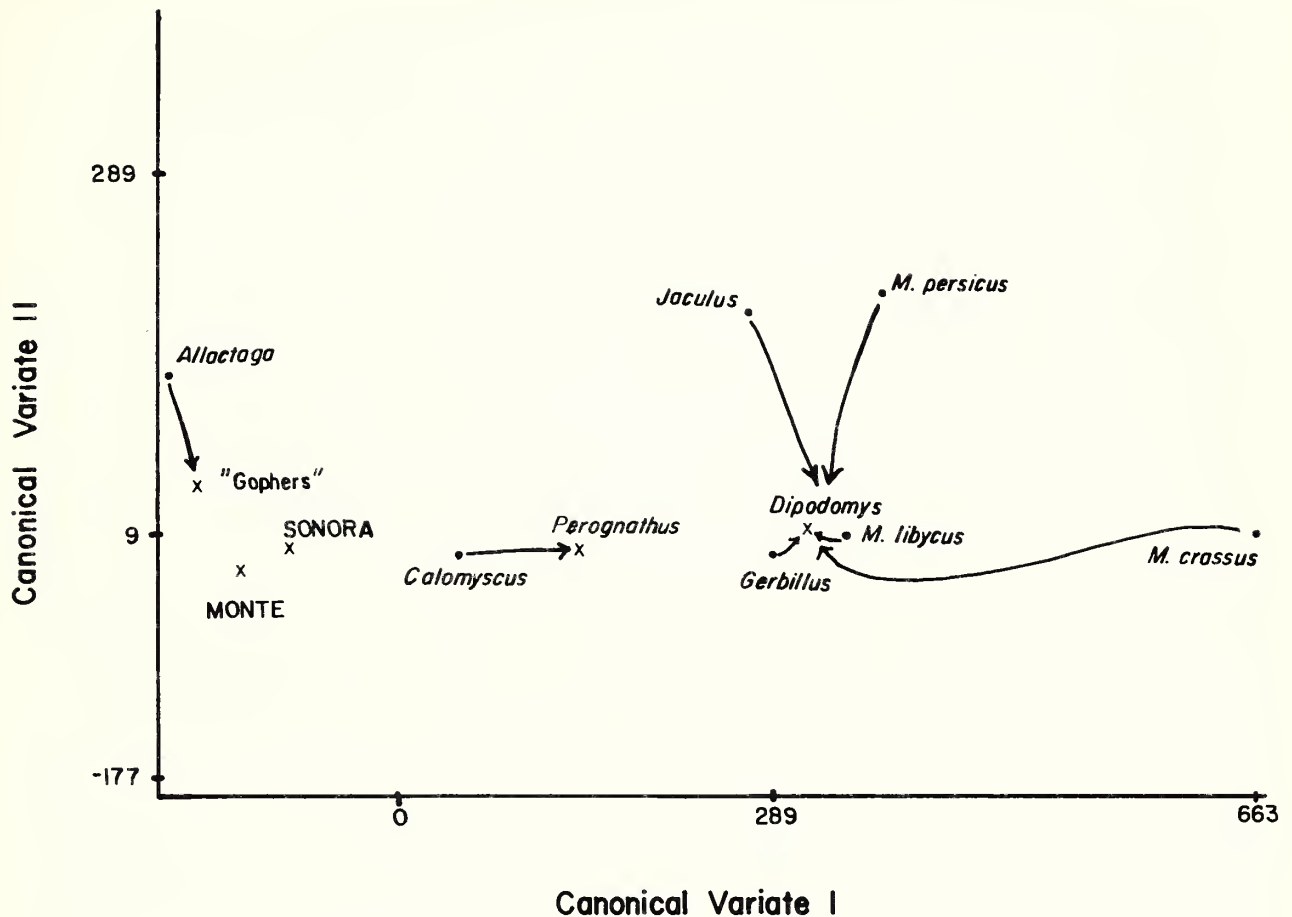
Fig. 11.—A canonical analysis of desert rodents from three localities based on dental traits. Iranian rodents have been assigned as unknowns, whereas North and South American species have been broken into a number of functional groups. Bipedal *Allactaga* is placed with the "gophers"; quadrupedal *Meriones libycus* is assigned to the *Dipodomys* groups. Symbols as in Fig. 10.

canonical axis (Table 8) show that the variables which made up that axis were primarily the molariform surface area, the possession of seizer-digger incisors, coronal hypsodonty, molar planation patterns, molar cusp patterns (for example, molar complexity), relative incisor width and incisor angle. Canonical Variate 2 was composed primarily of the molariform surface area, seizer-digger incisors, molar planation and complexity, coronal hypsodonty, relative incisor-molar length, and relative incisor width. Thus species with pronounced seizer-digger incisors or large molariform surface areas would have low values (strongly negative) on Canonical Variate 1, and the value of the canonical coefficient would increase as the molariform surface area, or the degree to which the incisors indicated a seizer-digger function, decreased. The great differences in the dental characteristics, and the great variability

of these traits, is apparent when the Mahalanobis Distances are examined—most are quite large when out-group comparisons are made.

The above analyses suggest that, within the So-

Table 6.—*The coefficients for each variable forming the first two canonical variates in Fig. 10.*

Original variable	Canonical variate 1	Canonical variate 2
TL/HBL	0.02	−0.04
HFL/HBL	−0.64	0.32
EL/HBL	0.71	0.49
VL/HBL	−0.27	−0.01
HL/HBL	0.28	−0.09
W	0.01	0.01
FB	3.86	0.20
TT	0.13	0.49
VD	−2.08	0.81
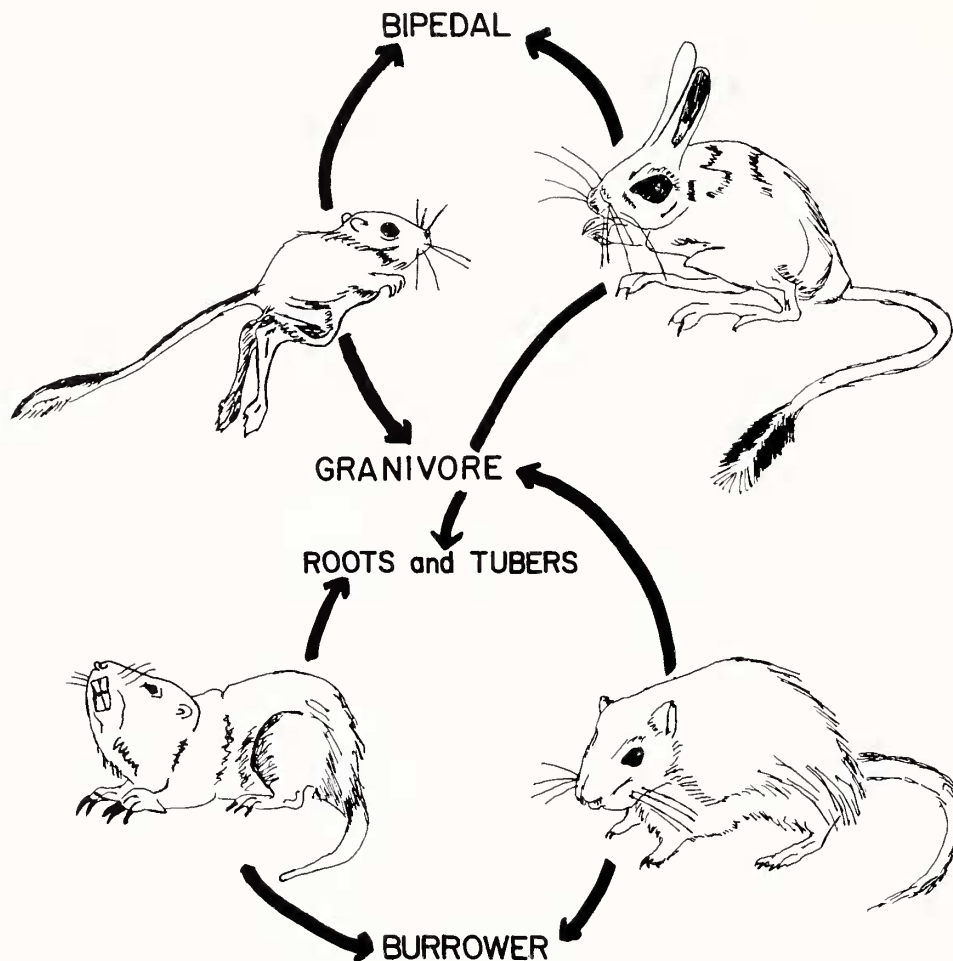
Fig. 12.—Bipedal desert rodents are found in both North America (*Dipodomys*) and Iran (*Allactaga,* upper right), whereas a highly fossorial group (*Thomomys,* lower left) inhabits North American deserts, and a less fossorial, but extensively burrowing species (*Meriones libycus,* lower right) is found in Iran. The food habits of the externally similar species are reversed, however. Niche segments (food and locomotion) have been switched.

Table 7.—*Square of Mahalanobis Distance (D²) of each of the groups and unknowns examined in an analysis of dental characteristics (Fig. 11). Mean ± SD.*

	Mean D² values				
	Dipodomys	*Perognathus*	Sonora	"Gophers"	Monte
Dipodomys	10.7 ± 0	*	*	*	*
Perognathus	*	12.0 ± 0	*	*	*
Sonora	*	*	14.0 ± 0	7572.5 ± 57.6	1863.9 ± 91.1
"Gophers"	*	*	7566.5 ± 22.6	8.0 ± 0	5072.4 ± 22.7
Monte	*	*	1862.0 ± 46.7	5076.4 ± 20.3	12.0 ± 0
Calomyscus	9131.5	*	*	*	*
Gerbillus	1384.2	*	*	*	*
Meriones libycus	1765.8	*	*	*	*
Meriones crassus	**	*	*	*	*
Meriones persicus	**	*	*	*	*
Allactaga	*	*	*	**	*
Jaculus	**	*	*	*	*

* Distance exceeded program printing capabilities.
** Assigned to this group although program printing capabilities were exceeded.

Fig. 13.—Serir habitat in Wadi Natroun, about 100 km NW of Cairo, where *Pachyuromys duprasi, Gerbillus perpallidus* (quadrupedal species), and *Jaculus jaculus* (a bipedal species) co-occur.

noran and Iranian deserts, both seed and root-and-tuber eating niche parameters are represented, and that bipedal, externally similar rodents are present in each desert, but food preferences and locomotor adaptations are associated in reversed ways (Fig. 12; that is, parts of each of these niche parameters have been switched). The Monte Desert, which contained bipedal, possibly granivorous rodentiform marsupials as recently as the late Pliocene or early Pleistocene, currently lacks obligate granivorous rodents or species which are bipedal (Figs. 14–16).

The causes of bipedality in desert rodents are not well understood, but a number of major factors (which are not necessarily mutually exclusive) have been suggested as possible causative agents, including predator avoidance and the freeing of the forelimbs for seed gathering (Bartholomew and Caswell, 1951; Vaughan, 1972; Hildebrand, 1974). One of the problems with invoking predator avoidance as a factor in the evolution of bipedality is that throughout the world most desert rodents are not bipedal. While it may be argued that bipedal forms live in areas of lower plant cover than quadrupedal species (for example, Price, 1978; Wondolleck, 1978), I have not found this to be the case. In Egypt, for example, bipedal *Jaculus jaculus* inhabits the same sparsely vegetated gravelly serir habitat as the quadrupedal *Pachyuromys duprassi* and *Gerbillus*

perpallidus (Fig. 13). In the southwestern United States, bipedal *Dipodomys deserti* and/or *D. merriami,* as well as the quadrupedal pocket mice, *Perognathus amplus* or *P. longimembris,* co-occur in exceedingly sparse habitats. Some bipedal species (for example, *Dipodomys agilis,* of the southwestern United States, which live under a dense canopy of chaparral vegetation, or *Microdipodops megacephalus,* near Mono Lake, California) may inhabit

Table 8.—*The coefficients for each of the original variables forming the first two canonical variates in Fig. 11.*

Original variable	Canonical variate 1	Canonical variate 2
W	1.3	0.1
IML/BL	−5.2	4.5
UI	4.8	−2.1
TRL/IML	−17.6	−0.1
TRL/BL	20.7	4.0
ZB/BL	−2.8	−0.3
IW/BL	−16.7	8.0
IL/BL	1.2	−3.0
IA	11.4	−7.0
SZ	−135.4	−42.5
MP	−45.1	−19.6
MC	31.7	17.0
TH	−16.5	−2.6
CH	71.1	18.2
MT	−37.2	0.8
SA	−408.4	−57.0
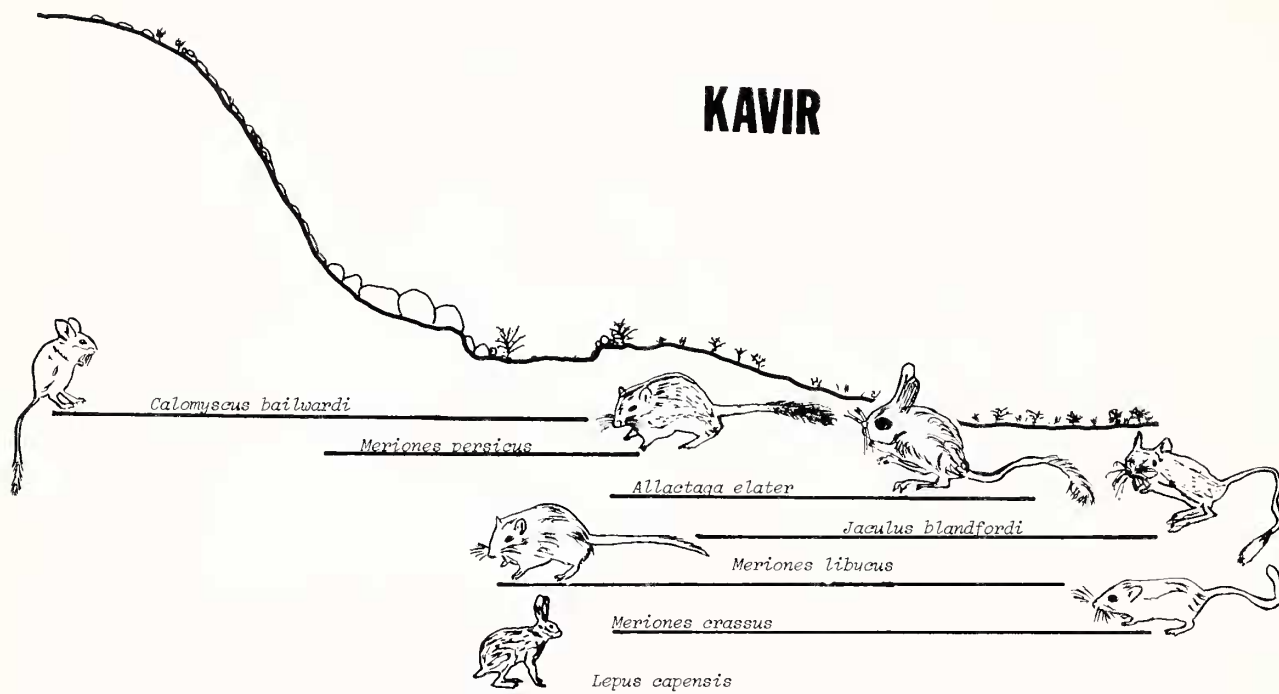
Fig. 14.—Representation of microhabitat selection of small mammals in the Dasht-e-Kavir Desert southeast of Tehran, a low scrub desert. In this and the following two figures, no attempt is made to designate abundance of a particular species within a particular microhabitat, nor are animals drawn to scale.
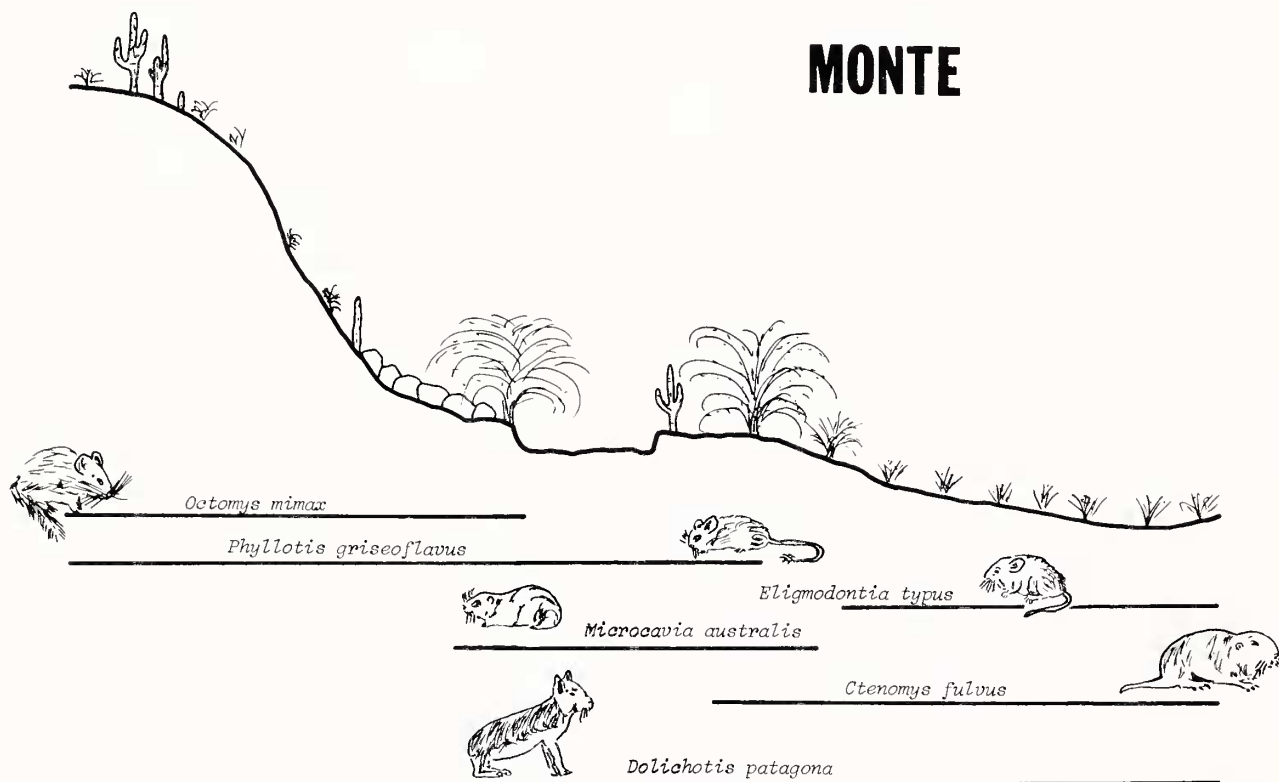

Fig. 15.—Microhabitat selection of rodents in the Monte Desert of northwestern Argentina, a floristically complex plant community.
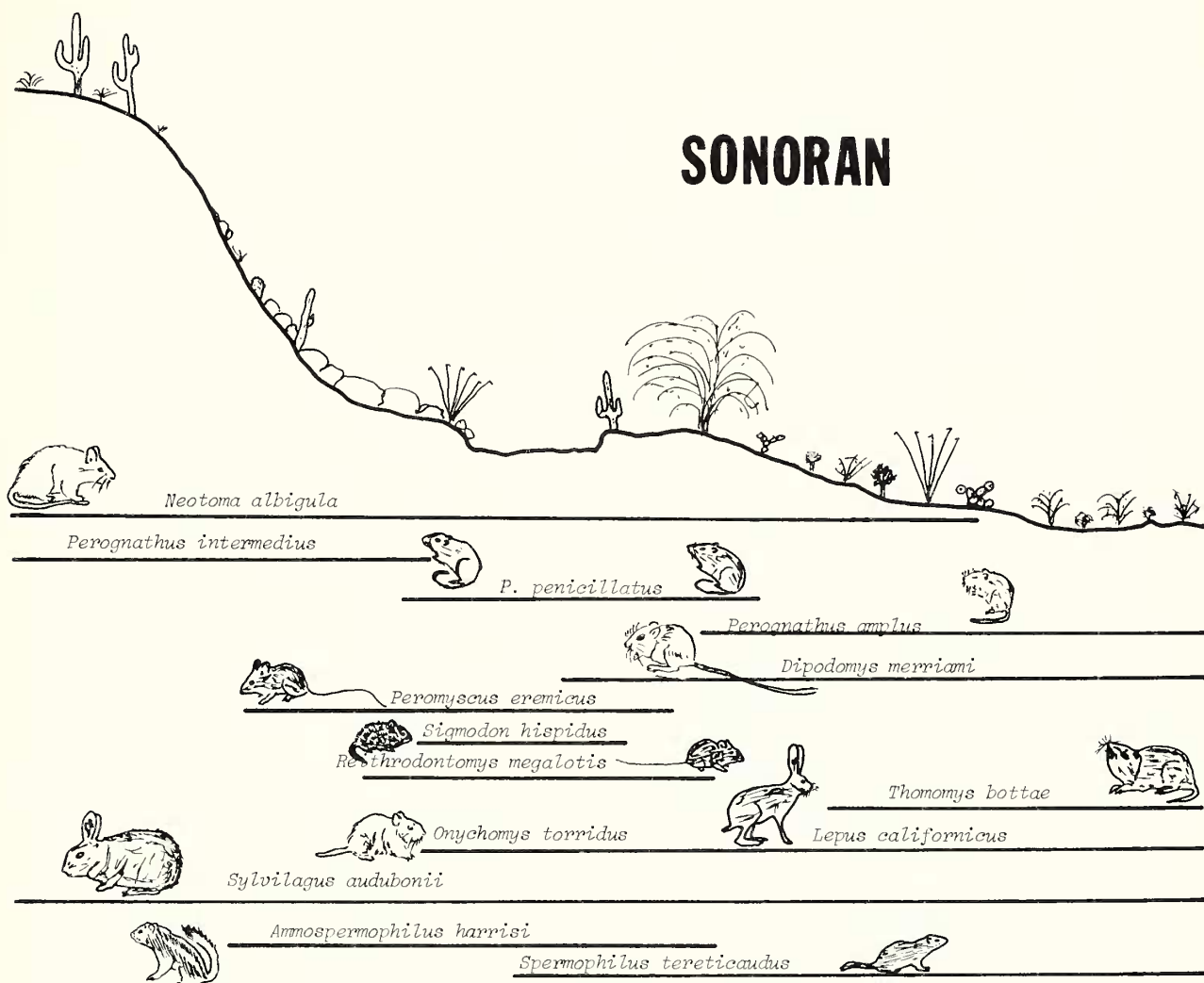
Fig. 16.—Microhabitat selection of small mammals in the Sonoran Desert near Tucson, Arizona.

localities supporting dense vegetation. The recent paper by Wondolleck (1978) presents data of foraging microhabitats of one bipedal species (*D. merriami*) and three quadrupedal coexisting species of *Perognathus*. These data suggest that the bipedal rodent forages in large open spaces devoid of vegetation while the three pocket mice forage in and around perrenial shrubs. Possibly bipedal species will be found to preferentially forage in areas where predator attacks would have a greater probability of success (open areas), while quadrupedal species will primarily forage near cover, scampering quickly across intervening patches of open desert. Substrate does not seem to be related to the bipedal habit. Some species, such as *D. agilis* of the chaparral scrub of California, occur on hard, clayey hillsides, while other species may be found on soils ranging from sand to gravel (for example, *M. megacephalus* on sand, *D. merriami* on some gravel slopes). Many quadrupeds are obligate granivores, and some bipeds eat vegetable material and insects.

Recently Reichman and Oberstein (1977) proposed that bipedality is a morphophysiological response for efficient and rapid locomotion to better exploit patchy, widely-spaced resources (see also Dawson, 1976; Price, 1978b). The niche reversal situation described here implies that among desert rodents granivory and bipedality may not be as obligately associated as has been supposed. Although it is possible that roots and tubers are more widely spaced in the sparse Iranian Desert than in the more vegetated Sonoran Desert, thus selecting for a "go-
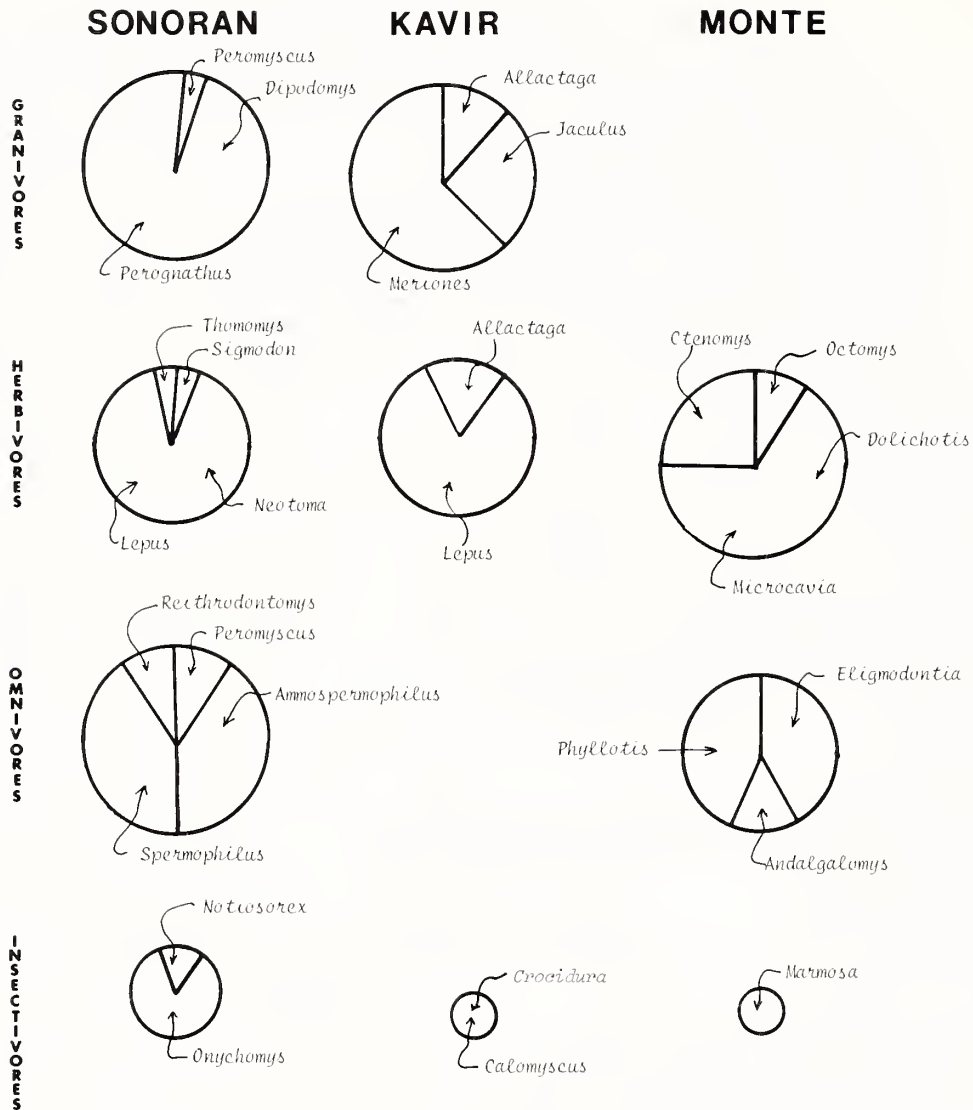
Fig. 17.—A subjective designation of the major food categories of small mammals in the Sonoran, Iranian, and Monte deserts. Note that granivory is lacking in the Monte, whereas herbivory predominates there. Insectivory is a minor trophic category in all deserts, being filled by a rodent and a shrew in both Arizona and Iran, and a marsupial in Argentina. The relative sizes of the circles within a food category are strictly my subjective estimate of the importance of that category in each desert. Thus, herbivory seems most important in the Monte, whereas seeds are about equally as important in the two northern deserts.

pher'' of high mobility (that is, a bipedal gopher), there is almost no hard evidence to support the supposed correlation of bipedality and the strategy of foraging on clumped resources. I have evidence from experimental field studies on desert rodents of the southwestern United States that bipedal and quadrupedal species forage on patchy and fine-grained resources in much the same manner, and that both groups concentrate on the finely-distributed seeds (Mares, unpublished). For the moment, the major selective forces affecting the evolution of bipedality among desert rodents are unknown.

There are many similarities between the Iranian and Sonoran desert rodent faunas, particularly in some of the overall morphological adaptations and the food habit specializations. Generally there were great similarities in the ecological relationships depicted by the distance and correlation phenograms, particularly the rather close clustering of *Onychomys* and *Calomyscus*. Although little is known about the natural history of the long-tailed hamster of Iran, Lay (1967) reports that some individuals fed primarily on seeds, whereas Walker (1964) notes that they readily consume animal material.

Table 9.—*Phylogenetic listing of desert rodents of the world used in multivariate analyses. Approximate location of capture given. Classification based on Simpson (1945) and Wood (1955).*

Suborder Sciuromorpha
  Family Sciuridae
    Xerus (Ghana: Damango)
    Geosciurus (Bechuanaland)
    Spermophilopsis leptodactylus (USSR, Turkmen)
    Ammospermophilus harrisi (southwestern U.S.)
  Family Geomyidae
    Thomomys bottae (southwestern U.S.)
    Pappogeomys castanops (southwestern U.S.)
  Family Heteromyidae
    Dipodomys merriani (southwestern U.S.)
    Dipodomys ordii (southwestern U.S.)
    Dipodomys spectabilis (southwestern U.S.)
    Dipodomys microps (southwestern U.S.)
    Dipodomys agilis (southwestern U.S.)
    Dipodomys deserti (southwestern U.S.)
    Microdipodops megacephalus (southwestern U.S.)
    Perognathus baileyi (southwestern U.S.)
    Perognathus intermedius (southwestern U.S.)
    Perognathus penicillatus (southwestern U.S.)
    Perognathus flavus (southwestern U.S.)

Suborder Myomorpha
  Family Cricetidae
  Subfamily Cricetinae
  Tribe Hesperomyini
    Reithrodontomys megalotis (southwestern U.S.)
    Reithrodontomys fulvescens (southwestern U.S.)
    Peromyscus eremicus (southwestern U.S.)
    Peromyscus maniculatus (southwestern U.S.)
    Peromyscus crinitus (southwestern U.S.)
    Baiomys taylori (southwestern U.S.)
    Onychomys torridus (southwestern U.S.)
    Eligmodontia typus (Argentina)
    Phyllotis griseoflavus (Argentina)
    Sigmodon hispidus (southwestern U.S.)
    Neotoma lepida (southwestern U.S.)
    Neotoma albigula (southwestern U.S.)
  Tribe Cricetini
    Calomyscus bailwardi (Iran)
    Phodopus roborowskii (China)
    Mystromys albicaudatus (South Africa)
    Cricetulus barabensis (China)
    Cricetulus curtatus (Mongolia)
  Subfamily Gerbillinae
    Gerbillus nanus (Iran)
    Gerbillus campestris (Morocco)
    Gerbillurus paeba (Southwest Africa)
    Sekeetamys calurus (Egypt)
    Taterillus harringtoni (Kenya)
    Desmodillus auricularis (?)
    Pachyuromys duprasi (Egypt)
    Meriones libycus (Iran)
    Meriones crassus (Iran)
    Meriones persicus (Iran)
    Psammomys obesus (Libya)
    Rhombomys opimus (China)

Table 9.—*Continued.*

  Family Spalacidae
    Spalax ehrenbergi (Egypt)
  Family Muridae
  Subfamily Murinae
    Thallomys nigricaudata (British East Africa)
    Leggadina delicata (Australia)
    Notomys alexis (Australia)
    Notomys carpentarius (Australia)
  Subfamily Dendromurinae
    Malacothrix typicus (Kalahari)
    Petromyscus barbour (South Africa)
    Steatomys athi (British East Africa)
  Family Dipodidae
  Subfamily Dipodinae
    Dipus sowerbyi (Mongolia)
    Paradipus ctenodactylus (U.S.S.R.)
    Eremodipus lichtensteini (U.S.S.R.)
    Stylodipus andrewsi (Mongolia)
    Jaculus blandfordi (Iran)
    Jaculus orientalis (Morocco)
    Jaculus deserti (Morocco)
    Scirtopoda telum (U.S.S.R.)
    Allactaga mongolica (Mongolia)
    Allactaga elater (Iran)
    Pygeretmus shitkovi (U.S.S.R.)
  Subfamily Cardiocraniinae
    Cardiocranius paradoxus (Mongolia)

Suborder Caviomorpha
  Family Caviidae
    Microcavia australis (Argentina)
  Family Octodontidae
    Octodon degus (Chile)
    Octomys mimax (Argentina)
    Octodontomys simonsi (Bolivia)
  Family Ctenomyidae
    Ctenomys fulvus (Argentina)

Suborder Bathyergomorpha
  Family Bathyergidae
    Bathyergus janetta (South Africa)
    Georhychus capensis (South Africa)
    Cryptomys darlingi (Southwest Africa)
    Heterocephalus glaber (Kenya)

Suborder ?Sciuromorpha, Hystricomorpha, or Myomorpha
  Family Ctenodactylidae
    Ctenodactylus gundi (Morocco)

The clustering of the hamster with the principally insectivorous-carnivorous *Onychomys* suggests that the propensity to eat animal matter may be more important than has previously been realized. Although *Calomyscus* bears a strong resemblance to *Peromyscus* (Osgood, 1947), the multivariate analyses were usually able to separate the hamster from the *Peromyscus* assemblage. *Jaculus blandfordi* is an uncommon species that is very poorly

Table 10.—*Regional listing of the genera comprising each desert rodent fauna used in the multivariate analyses.*

North America	South America	Australia	Northern Africa	Southern Africa	China	U.S.S.R.	Iran
Dipodomys	*Ctenomys*	*Leggadina*	*Heterocephalus*	*Thallomys*	*Cricetulus*	*Stylodipus*	*Calomyscus*
Microdipodops	*Octomys*	*Notomys*	*Xerus*	*Geosciurus*	*Phodopus*	*Dipus*	*Gerbillus*
Perognathus	*Octodon*		*Pachyuromys*	*Steatomys*	*Dipus*	*Spermophilopsis*	*Meriones*
Neotoma	*Octodontomys*		*Sekeetamys*	*Desmodillus*	*Cardiocranius*	*Pygeretmus*	*Allactaga*
Onychomys	*Microcavia*		*Psammomys*	*Malacothrix*	*Allactaga*	*Paradipus*	*Jaculus*
Peromyscus	*Phyllotis*		*Spalax*	*Petromyscus*	*Rhombomys*	*Eremodipus*	*Rhombomys*
Baiomys	*Eligmodontia*		*Taterillus*	*Georhychus*		*Scirtopoda*	
Reithrodontomys			*Ctenodactylus*	*Bathyergus*		*Alactagulus*	
Sigmodon			*Jaculus*	*Cryptomys*		*Allactaga*	
Ammospermophi- lus			*Gerbillus*	*Mystromys*		*Rhombomys*	
Thomomys				*Gerbillurus*			
Pappogeomys							

known ecologically. Other species of *Jaculus* are known to eat seeds as well as other plant material (Petter, 1961; Ognev, 1963; Eisenberg, 1975), and the particular diet probably varies greatly from species to species. At least one species, *J. turcmenicus* of the U.S.S.R., is almost totally herbivorous (Naumov and Lobachev, 1975). The multivariate analyses suggest that *J. blandfordi* is closer ecologically to *Dipodomys* than is *Allactaga*. *Gerbillus nanus* is probably quite similar ecologically to *Perognathus* and was clustered with the pocket mouse group in both distance and correlation analyses. Schematic representations of some of the broad niche categories of rodents at the Kavir, Sonoran, and Monte desert localities are given in Figs. 14–17.

The fact that only one rodent from the Monte Desert was clustered with Iranian and Sonoran species within the desert specialist category supports the contention that the South American species have not had time to evolve a high degree of adaptation to desert conditions. This is particularly true for the cricetines, descendants of the most recent colonizers of the South American continent.

An Analysis of the Desert Rodents of the World

The previous analyses yielded a number of results that, in retrospect, either appeared logical when I had an intimate knowledge of the ecology of the various species being examined, such as in the Monte-Sonora-New Mexico Forest comparison, or were counterintuitive when the fauna was less well known ecologically, for example in the Sonora-Monte-Iranian study. The anomalous relationship of the bipedal herbivorous *Allactaga* finds at least some support in the literature, whereas the similarities between *Meriones* and *Dipodomys* in overall food habits have been shown in a number of studies. I decided to measure individuals of as many species of desert rodents as possible in order to determine whether or not these same multivariate techniques utilizing various suites of morphoecological characteristics could be extended to the world desert system. If the information produced by such analyses reflects aspects of the biology of the species, it should allow one to determine which species in the various disjunct deserts might fill similar roles, as well as which species are

Table 11.—*Mean Mahalanobis Distances (D^2) of each desert fauna to all other faunas when 40 traits are utilized (Fig. 18).*

	U.S.	South America	Australia	North Africa	South Africa	China	Russia	Iran
U.S.	25.0	55.0	110.2	43.4	39.2	76.2	76.8	62.4
South America	—	25.5	113.9	70.8	72.6	86.1	83.9	68.1
Australia	—	—	27.4	117.7	101.9	97.1	103.3	100.7
North Africa	—	—	—	29.8	40.5	85.7	83.3	68.5
South Africa	—	—	—	—	30.3	73.4	77.9	70.6
China	—	—	—	—	—	29.7	46.8	71.8
Russia	—	—	—	—	—	—	28.1	70.1
Iran	—	—	—	—	—	—	—	26.7
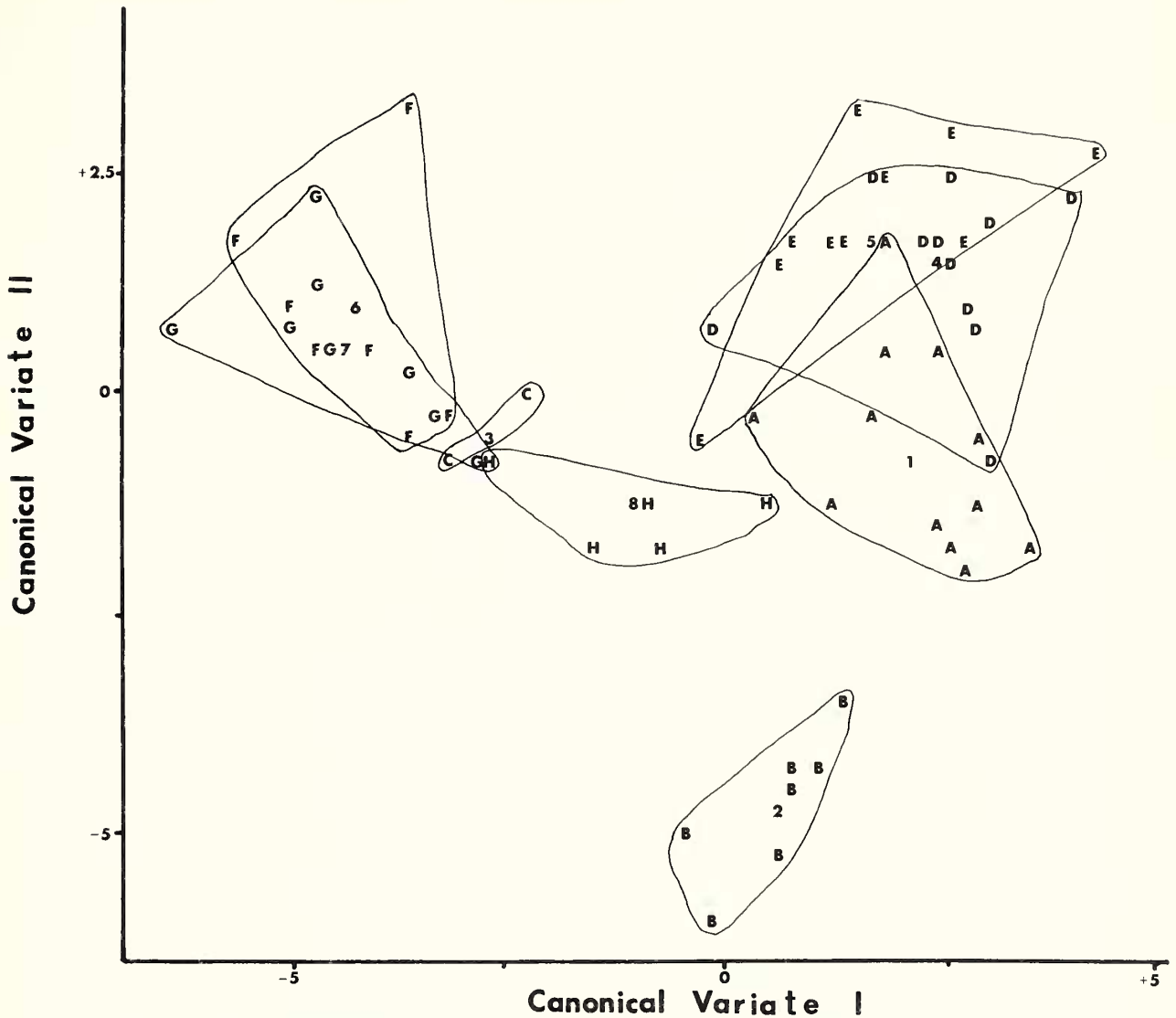
Fig. 18.—Canonical analysis of desert rodent faunas from eight regions based on 40 morphological traits. Symbols: number 1 and letters A indicate the group mean and individual cases respectively, for United States desert rodents; 2 and B = South America; 3 and C = Australia; 4 and D = North Africa; 5 and E = South Africa; 6 and F = China, 7 and G = Russia; 8 and H = Iran. One species per genus occurring in each desert region (and listed in Table 9) was used in the analysis so as not to weight any particular genus more than any other.

unique to a particular desert and seem to fill a niche which is not even loosely repeated in any other desert of the world. Further, it might be possible to compare the degree of desert adaptation of the various rodent faunas and correlate this with the time span over which desert adaptations have occurred. Although I was not able to examine every known species of desert rodent, most genera and many species are represented in the analyses that follow (Tables 9 and 10). Basically, rodent faunas from eight major desert regions were examined. In many

cases the results are only tentative (and essentially predictions) since the majority of species are very poorly known ecologically.

When the genera and species are grouped by desert region and compared with one another (one species/genus) utilizing all 40 morphological characteristics, the South American desert is widely separated from all other desert regions along the second canonical axis (Fig. 18, Tables 11 and 12). The North American, North African, and South African deserts are closely clustered, as are the

Table 12.—*Coefficients for the first two canonical variates shown in Fig. 18.*

Original variable	Canonical variate 1	Canonical variate 2
HBL	0	0
TL	0	0
HFL	.2	.1
EL	.2	.2
VL	0	.1
HL	−.3	−.2
TL/HBL	0	0
HFL/HBL	−.1	−.1
EL/HBL	−.4	−.3
VL/HBL	0	0
HL/HBL	.5	.2
FB	−1.6	−.2
TT	−.3	−.3
UL	−.1	−.3
UW	.1	−.3
MW	−1.0	.6
1L	.8	.7
U1	.4	.4
TRL	.2	−1.3
TRL/1ML	−.2	−.1
TRL/BL	.5	−.1
ZB/BL	−.1	.2
1L/BL	.1	−.3
1A	.7	.8
SZ	1.6	.1
MP	.9	0
TH	−.1	.2
CH	−2.0	−.2
MT	−.4	−.8
VD	.9	−.4
TW	−3.5	−1.4
SA	−.2	0

Table 13.—*Coefficients for the first two canonical variates shown in Fig. 19.*

Original variable	Canonical variate 1	Canonical variate 2
BL	.2	−.5
1ML	.2	.5
MW	.5	.5
1W	0	1.6
TRL	−2.1	−.9
TRL/1ML	.1	.3
ZB/BL	.1	−.1
IW/BL	.1	−.9
1L/BL	−.1	0
1A	.1	−.7
SZ	.1	−.9
T1	−.7	−.1
MP	−.7	−.1
MC	−.4	.2
TH	.5	−.1
CH	1.3	.9
MT	−1.0	−.1
TW	1.0	.7
SA	.1	0

China and Russian assemblages, while the Iranian desert rodent fauna seems to bridge a gap between the African and Asian faunas. Australia is located between Iran and the China-Russia cluster. One North American species, *Baiomys taylori*, was assigned to the South African fauna. The mean Mahalanobis Distances of each species within a particular fauna to the faunal mean values of the other groups (Table 12) show that the highly desert specialized groups are close to one another (for example, the United States-North Africa distance, versus the United States-South America distance), while South America is closest to its phylogenetically most similar assemblage, North America. The South American fauna is located low on Canonical Variate 2 where such variables as molariform toothrow width, molar triangulation, proodont or orthodont incisors, and molariform toothrow length, are weighted heavily. The preponderance of herbivory

as opposed to granivory or insectivory among the Monte rodents (Fig. 17) thus seems to distinguish them from the other desert faunas.

The same desert groups were analyzed using 23 dental traits (Fig. 19, Tables 13 and 14), 27 non-ratio traits (Fig. 20, Tables 15 and 16), and 25 morphoecological characteristics (Fig. 21, Tables 17 and 18). The basic pattern shown in the 40 trait analysis is repeated in that the South American rodents are always separated from the other groups, and Russia and China are usually plotted closely together. North America is generally located quite close to North Africa, and Australia, which contains only three rodents, is either placed with the China-Russia groups, or with the Iranian fauna. The Russia and China groups contain the most bipedal forms (Dipodidae), with herbivores such as *Dipus*, *Eremodipus*, *Stylodipus*, and *Allactaga*, and quadrupedal herbivores such as *Cricetulus*, *Phodopus*, or *Rhombomys*. Herbivory and bipedality are the major strategies among rodents of these two regions. Iran actually is more like Africa (and thus North America) as far as the overall rodent assemblage is concerned, although it shares some generic affinities with the Asian deserts to the north and east. Nevertheless, its location in most analyses as either being similar to the African-North American groups, or positioned between the African and Asian faunas, seems logical, and probably reflects both its phylogenetic affinities (to the Asian faunas),
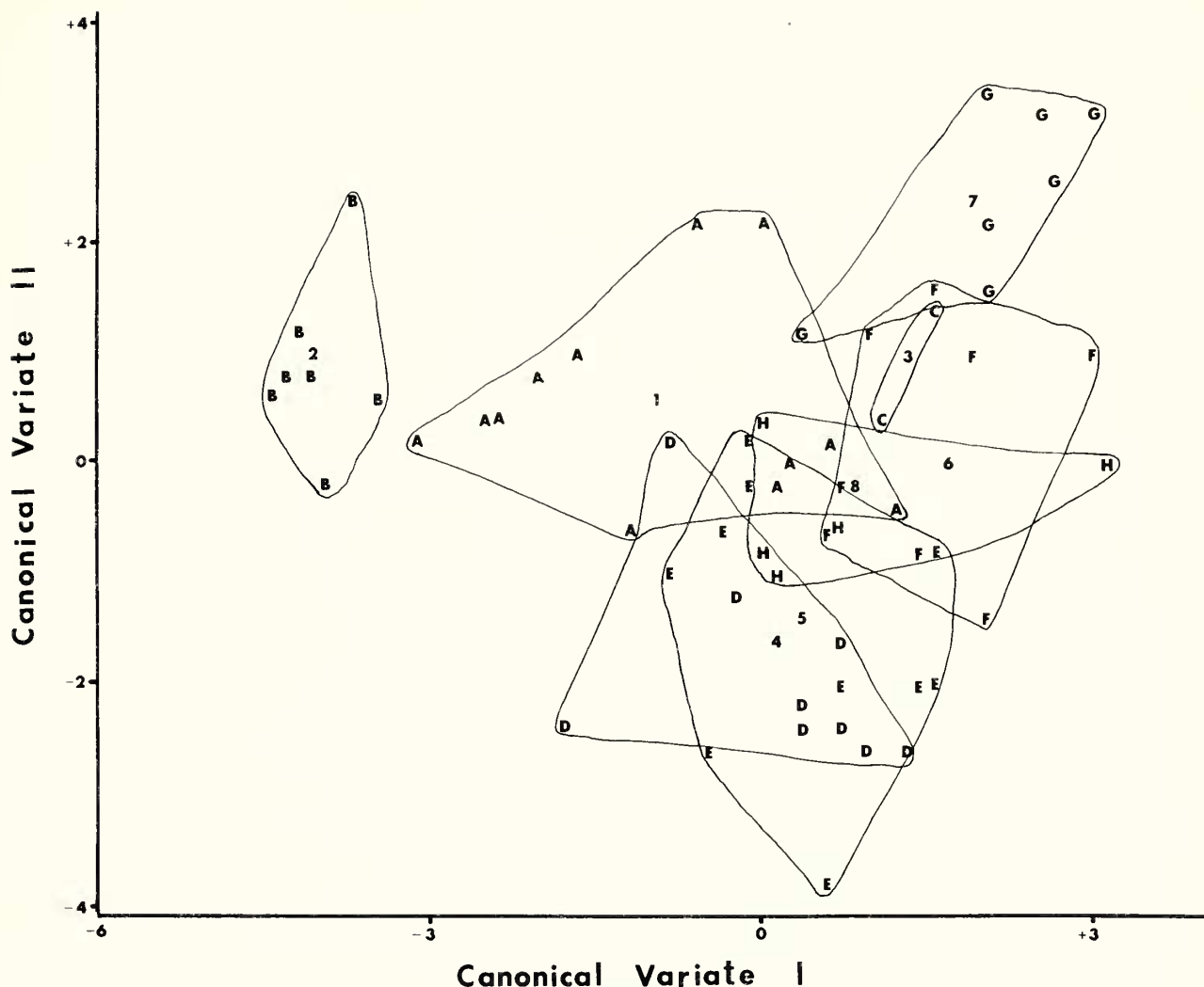
Fig. 19.—Canonical analysis of desert rodent faunas from eight regions based on 23 dental traits. Symbols as in Fig. 18.

as well as its ecological affinities (to the North African and North American faunas).

I showed earlier that cluster analysis is a useful technique for examining evolutionary convergence. Presumably, those species sharing a large number of traits will be grouped closely together. If they are only distantly phylogenetically related, then those that are clustered together may be considered species that are convergent. Since many of the traits utilized in these analyses are morphoecolog-

Table 14.—*Mean Mahalanobis Distances (D²) of each desert fauna to all other faunas when 23 dental traits are utilized (Fig. 19).*

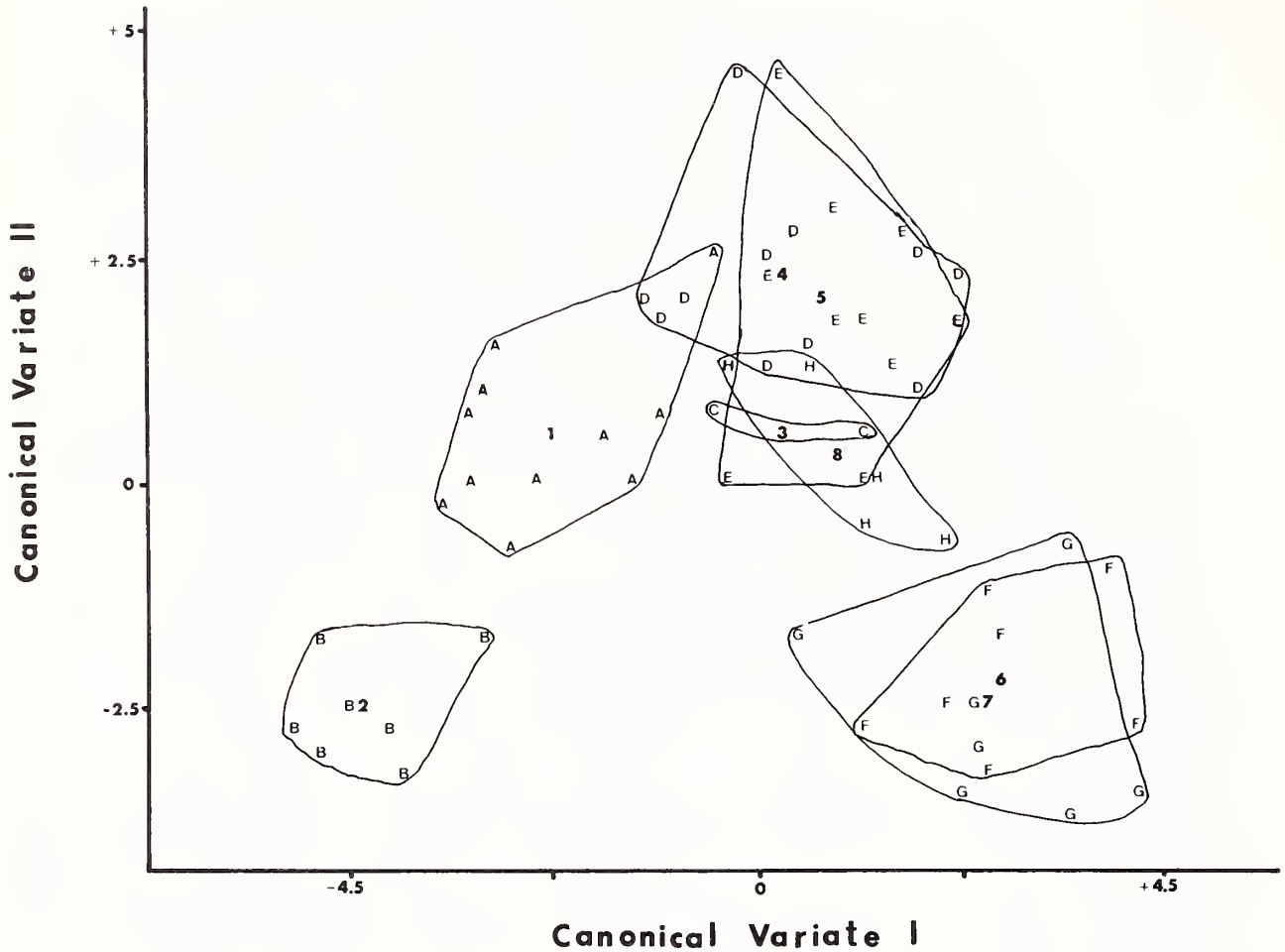|	U.S.	South America	Australia	North Africa	South Africa	China	Russia	Iran
U.S.	15.9	30.7	65.7	37.3	23.7	29.5	30.9	25.6
South America	—	13.9	75.9	40.9	41.2	49.5	54.2	46.5
Australia	—	—	27.2	76.5	69.0	69.1	74.3	78.7
North Africa	—	—	—	18.4	24.8	32.1	38.7	29.7
South Africa	—	—	—	—	16.7	24.9	37.0	27.2
China	—	—	—	—	—	13.3	27.0	27.1
Russia	—	—	—	—	—	—	17.6	32.2
Iran	—	—	—	—	—	—	—	14.6

Fig. 20.—Canonical analysis of desert rodent faunas from eight regions based on 27 non-ratio traits. Symbols as in Fig. 18.

ical ones, thus strongly implying some ecological function, species forming a cluster can be considered ecological equivalents for those ecological traits reflected in their morphology. Although both distance and correlation phenograms (Sneath and Sokal, 1973) were determined for each group of measurements, I will use only one or the other of these to illustrate the resultant clusters, particularly since differences between the two clustering techniques were relatively minor. I will briefly describe the clusters in each phenogram before discussing my overall impressions of convergent evolution in desert rodents derived from the various analyses.

The 40-character distance phenogram listing all of the 78 species of desert rodents is shown in Fig. 22; the cophenetic correlation coefficient is 0.83, indicating that the 2-dimensional representation of the 40-dimensional relationship is not greatly dis-

torted. There are eight major clusters composed of numerous smaller clusters. The first includes kangaroo rats of the genus *Dipodomys* (Family Heteromyidae) of the Sonoran, Mojave, and Great Basin deserts and the chaparral scrublands of California. *Sekeetamys calurus* (Cricetidae) of the Egyptian Sahara Desert is closely clustered with *Dipodomys*. The dipodids, *Jaculus orientalis* and *J. deserti* of the Sahara, *Stylodipus andrewsi* of Mongolia, and *Scirtopoda telum* and *Eremodipus lichtensteini* of the U.S.S.R., form a second small cluster. The caviomorph octodontids *Octomys mimax* of the Argentine Monte, and *Octodontomys simonsi* of the Bolivian altiplano, are loosely clustered with *Rhombomys opimus* (Cricetidae) from China and Iran. Completing the first major cluster is a loose grouping of the dipodids, *Dipus sowerbyi* of Mongolia and *Paradipus ctenodactylus* of the
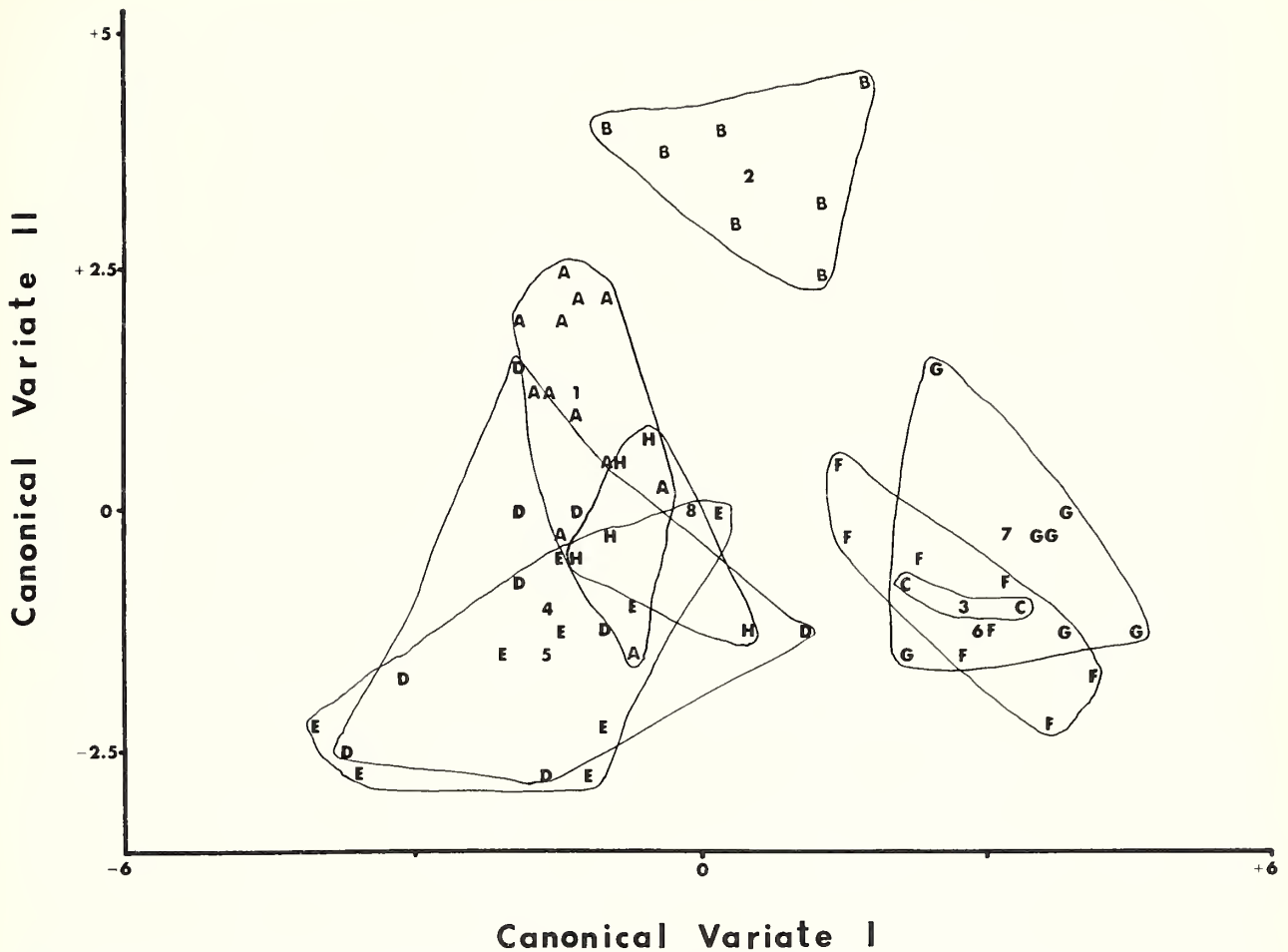
Fig. 21.—Canonical analysis of desert rodent faunas from eight regions based on 25 morphoecological traits. Symbols as in Fig. 18.

U.S.S.R. Basically species in this assemblage are highly desert specialized, medium-sized rodents, having a pronounced inflation of the auditory bullae and reduced pinnae; most are bipedal.

The second cluster is a small group composed of the caviomorphs *Microcavia australis* (Caviidae) of the Argentine Monte, and *Octodon degus* (Octodontidae) of the arid region of Chile, and the ctenodactylid *Ctenodactylus gundi* from the Sahara of Morocco. These animals are similar in body size and overall proportions; all frequent rock piles and other rocky areas, with *M. australis* apparently being the most labile in habitat requirements (see Walker, 1964; Mares, 1973; Glanz, 1977; Meserve and Glanz, 1978). All three species are herbivorous.

The third major cluster is a large one composed of numerous smaller clusters. The first of these contains the small granivores, *Perognathus* (Heteromyidae) of the United States, and *Gerbillus nanus*

(Cricetidae) of Iran, which are loosely clustered with the small heteromyid bipedal granivore, *Microdipodops megacephalus* of North America. Because many traits used in the 40-character analysis are correlated with overall body size, this parameter has a great influence on the final depiction of relationships. Interestingly however, *Microdipodops* is grouped with *Perognathus*, rather than *Dipodomys* (which it resembles, externally); this is in accordance with suggested phylogenetic relationships (Hafner, 1978).

The next small cluster is comprised of the North American grasshopper mouse, *Onychomys torridus*, the Chinese dwarf hamster, *Phodopus roborowskii*, the Mongolian rat-like hamsters, *Cricetulus curtatus* and *C. barabensis*, and the white-tailed rat of South Africa, *Mystromys albicaudatus*. All of these are rather small quadrupedal cricetids; most apparently are seed eaters (Walker, 1964).

Dipodomys merriami
D. ordi
D. spectabilis
Sekeetamys calurus
D. microps
D. agilis
D. deserti
Jaculus orientalis
J. deserti
Stylodipus andrewsi
Scirtopoda telum
Eremodipus lichtensteini
Octomys mimax
Octodontomys simonsi
Rhombomys opimus
R. opimus
Dipus sowerbyi
Paradipus ctenodactylus
Microcavia australis
Octodon degus
Ctenodactylus gundi
Microdipodops megacephalus
Perognathus baileyi
P. intermedius
P. penicillatus
P. flavus
Gerbillus nanus
Onychomys torridus
Cricetulus barabensis
Phodopus roborowskii
Mystromys albicaudatus
Cricetulus curtatus
Peromyscus eremicus
P. maniculatus
Reithrodontomys fulvescens
R. megalotis
Eligmodontia typus
Petromyscus barbour
Baiomys taylori
Steatomys athi
Peromyscus crinitus
Taterillus harringtoni
Gerbillus campestris
Gerbillurus paeba
Notomys alexis
Notomys carpentarius
Malacothrix typicus
Calomyscus bailwardi
Cardiocranius paradoxus
Neotoma albigula
N. lepida
Sigmodon hispidus
Phyllotis griseoflavus
Ammospermophilus harrisi
Pachyuromys duprasi
Desmodillus auricularis
Thallomys nigricaudata
Psammomys obesus
Meriones libycus
M. crassus
Allactaga mongolica
Pygeretmus shitkovi
Alactagulus pumilio
Allactaga elater
Meriones persicus
Jaculus blandfordi
Thomomys bottae
Ctenomys fulvus
Spalax ehrenbergi
Pappogeomys castanops
Bathyergus janetta
Georhychus capensis
Cryptomys darlingi
Heterocephalus glaber
Xerus
Geosciurus
Spermophilopsis leptodactylus
Leggadina delicata

1.7   1.3   .9   .5   .1

DISTANCE

Table 15.—Coefficients for the first two canonical variates shown in Fig. 20.

Original variable	Canonical variate 1	Canonical variate 2
HBL	0	.1
TL	0	0
HFL	−.1	−.1
EL	0	0
VL	.1	0
HL	−.2	−.3
FB	1.4	−.5
TT	.1	−.2
BL	.1	0
IML	0	0
UL	.1	0
UW	−.3	.5
MW	.4	−.1
ZB	.6	0
IW	−.2	−.4
IL	−.5	0
TRL	−1.5	−1.7
IA	.4	.8
SZ	−.3	2.3
TI	−1.2	−.1
MP	−.1	−.2
MC	−.6	−.9
TH	.4	.1
CH	−1.2	−.1
MT	−.9	−1.1
VD	−1.1	.3
TW	1.0	.8

Small, quadrupedally-scansorial omnivores form the next small cluster. Included are *Peromyscus* and *Reithrodontomys* of North America; *Eligmodontia typus* of Argentina; *Petromyscus barbour* of South Africa; the North American (Chihuahuan Desert) pygmy mouse, *Baiomys taylori*; and the South African fat mouse, *Steatomys athi*. All of these are cricetids.

The last subcluster composing the third major cluster is comprised of three groups. North American *Peromyscus crinitus*, and the North African gerbils (*Taterillus harringtoni*, *Gerbillus campestris*, and *G. paeba*) are grouped together and attached to the second subcluster which includes the murid Australian hopping mice, *Notomys alexis* and *N. carpentarius*. The South African gerbil mouse, *Malacothrix typicus*, and the Iranian hamster, *Calomyscus bailwardi*, comprise the third subcluster.

←

Fig. 22.—Distance phenogram resulting from a cluster analysis of 78 species of desert rodents utilizing 40 morphological characteristics.
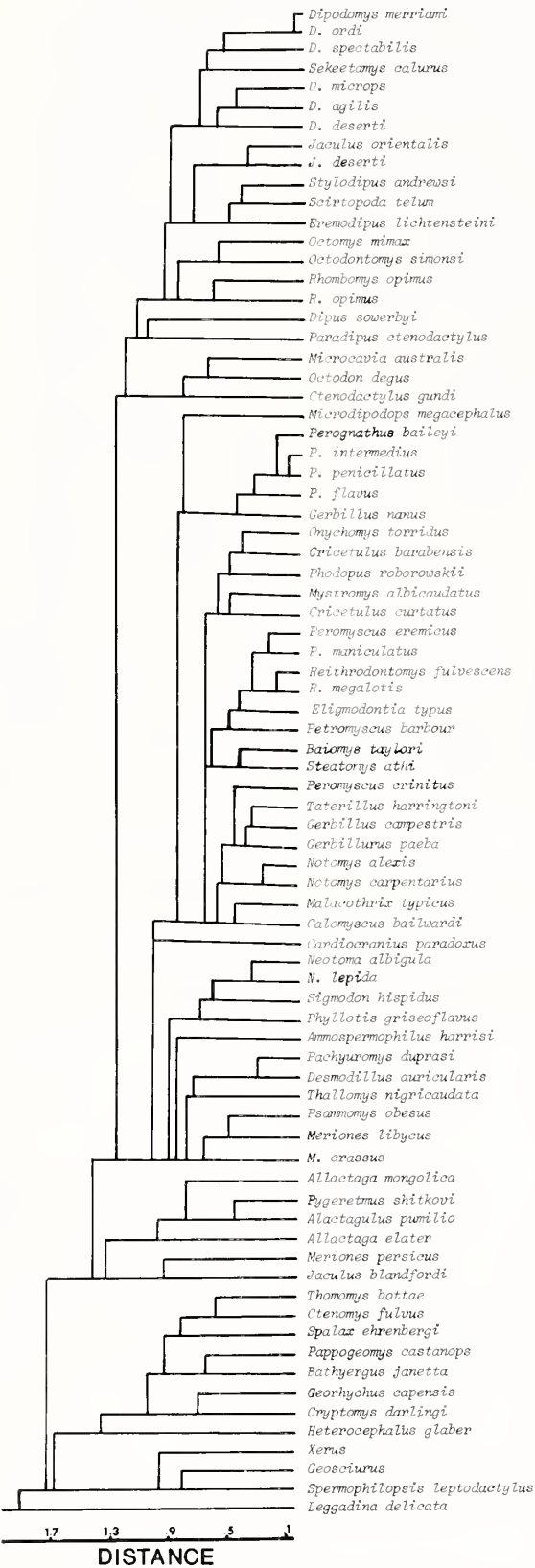
Table 16.—*Mean Mahalanobis Distances (D^2) of each desert fauna to all other faunas when 27 non-ratio traits are utilized (Fig. 20).*

	U.S.	South America	Australia	North Africa	South Africa	China	Russia	Iran
U.S.	22.3	49.0	70.0	42.5	41.2	61.4	60.2	47.5
South America	—	24.0	81.6	71.0	73.2	81.3	78.6	74.6
Australia	—	—	21.1	55.3	54.6	67.8	71.8	56.4
North Africa	—	—	—	25.2	31.7	59.2	54.4	44.9
South Africa	—	—	—	—	25.2	49.4	54.5	44.0
China	—	—	—	—	—	23.2	36.2	50.1
Russia	—	—	—	—	—	—	23.6	49.0
Iran	—	—	—	—	—	—	—	20.2

Finally, the five-toed dwarf jerboa, *Cardiocranius paradoxus,* is very tenuously included within the third major cluster.

The fourth major cluster is composed of medium-sized, quadrupedal forms only loosely associated between subclusters. The North American wood rats and cotton rats, *Neotoma* and *Sigmodon,* respectively, are clustered with the South American leaf-eared mouse, *Phyllotis (Graomys) griseoflavus.* The North American sciurid, *Ammospermophilus harrisi* is not closely allied with other members of this cluster. Two smaller clusters, one containing the Sahara fat-tailed sand rat, *Pachyuromys duprasi*; the South African Cape short-eared gerbil, *Desmodilhis auricularis*; and the South African acacia rat, *Thallomys nigricaudata*; and the other including the Sahara sand rat, *Psammomys obesus*; and the two jirds, *Meriones libycus* and *M. crassus,* complete the major cluster.

The fifth large cluster is made up of two distinct subclusters. The first contains the jerboas—*Allactaga mongolica* of China; *Pygeretmus shitkovi* of the U.S.S.R.; *Allactaga elater* of Iran; and *Alactagulus pumilio* of the U.S.S.R. The second includes the large jird, *Meriones persicus,* and the dipodid, *Jaculus blandfordi.*
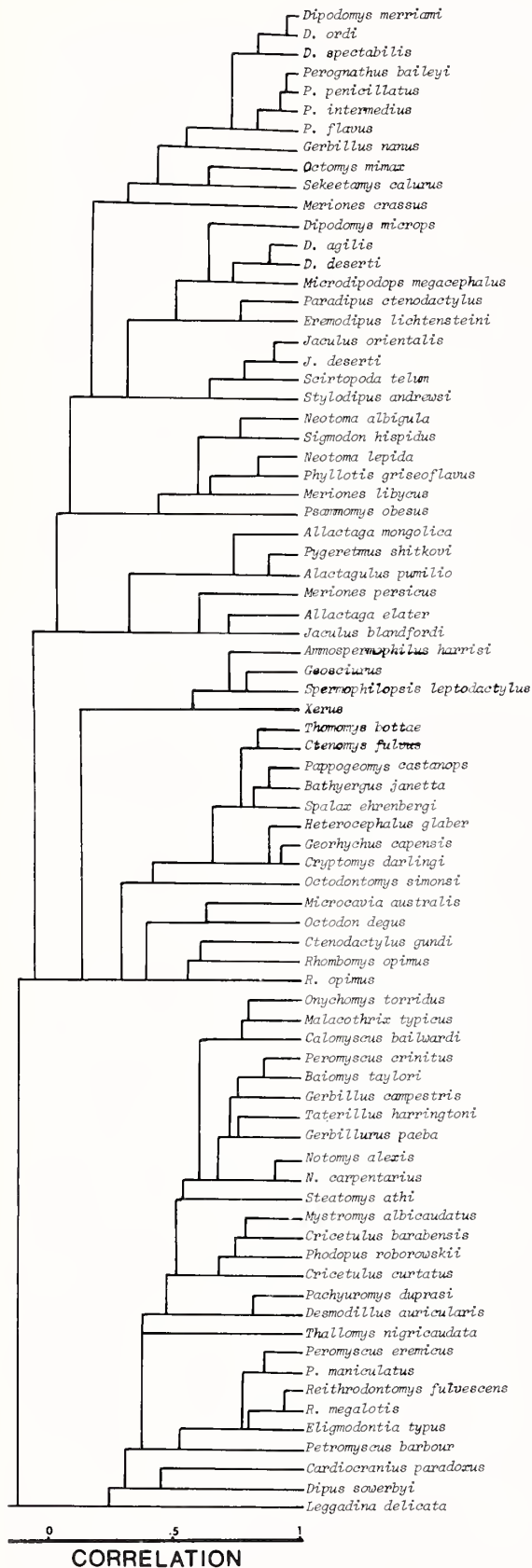
The sixth major cluster includes fossorial species of all types. *Thomomys bottae,* a North American gopher, is closely allied with the tuco-tuco of the Argentine Monte (*Ctenomys fulvus*), and these are connected to the Sahara mole rat, *Spalax ehrenbergi.* A second group, loosely joined to the first, is composed of another North American gopher, *Pappogeomys castanops,* and the South African bathyergid mole rat, *Bathyergus janetta.* The other two bathyergids, *Georhychus capensis* and *Cryptomys darlingi,* are clustered together and joined to the aforementioned fossorial species, while the naked mole rat of eastern Africa, *Heterocephalus glaber,* is loosely clustered with the other fossorial species, thus completing this major cluster.

The final cluster is a small one composed of sciurids—*Xerus* from North Africa; *Geosciurus* from South Africa; and *Spermophilopsis leptodactylus* from the U.S.S.R. Finally, the phenogram is completed with the inclusion of the Australian murid, *Leggadina delicata.*

When only 25 morphoecological traits are utilized in cluster analysis, a somewhat different picture of relationships is obtained. Six major clusters, many composed of a number of loosely associated subclusters, are evident in the correlation phenogram of Fig. 23 (cophenetic correlation coefficient = 0.763).

Table 17.—*Coefficients for the first two canonical variates shown in Fig. 21.*

Original variable	Canonical variate 1	Canonial variate 2
HBL	0	0
TL/HBL	0	0
HF/HBL	0	0
EL/HBL	0	.1
VL/HBL	0	0
HL/HBL	−.1	0
FB	1.2	−.1
TT	.6	0
TRL/BL	0	.1
UI	0	0
TRL/IML	.2	.2
TRL/BL	−.1	0
ZB/BL	.1	−.1
IW/BL	.1	−.1
IL/BL	−.2	.2
IA	−.5	−.4
SZ	−1.4	−1.5
TI	.4	−.5
MP	.2	.2
MC	0	.9
TH	.2	−.4
CH	.6	−.4
IA	.2	.7
VD	−.9	.4
SA	0	0

Dipodomys merriami
D. ordi
D. spectabilis
Perognathus baileyi
P. penicillatus
P. intermedius
P. flavus
Gerbillus nanus
Octomys mimax
Sekeetamys calurus
Meriones crassus
Dipodomys microps
D. agilis
D. deserti
Microdipodops megacephalus
Paradipus ctenodactylus
Eremodipus lichtensteini
Jaculus orientalis
J. deserti
Scirtopoda telum
Stylodipus andrewsi
Neotoma albigula
Sigmodon hispidus
Neotoma lepida
Phyllotis griseoflavus
Meriones libycus
Psammomys obesus
Allactaga mongolica
Pygeretmus shitkovi
Alactagulus pumilio
Meriones persicus
Allactaga elater
Jaculus blandfordi
Ammospermophilus harrisi
Geoscirus
Spermophilopsis leptodactylus
Xerus
Thomomys bottae
Ctenomys fulvus
Pappogeomys castanops
Bathyergus janetta
Spalax ehrenbergi
Heterocephalus glaber
Georhychus capensis
Cryptomys darlingi
Octodontomys simonsi
Microcavia australis
Octodon degus
Ctenodactylus gundi
Rhombomys opimus
R. opimus
Onychomys torridus
Malacothrix typicus
Calomyscus bailwardi
Peromyscus crinitus
Baiomys taylori
Gerbillus campestris
Taterillus harringtoni
Gerbillurus paeba
Notomys alexis
N. carpentarius
Steatomys athi
Mystromys albicaudatus
Cricetulus barabensis
Phodopus roborowskii
Cricetulus curtatus
Pachyuromys duprasi
Desmodillus auricularis
Thallomys nigricaudata
Peromyscus eremicus
P. maniculatus
Reithrodontomys fulvescens
R. megalotis
Eligmodontia typus
Petromyscus barbour
Cardiocranius paradoxus
Dipus sowerbyi
Leggadina delicata

0   .5   1
CORRELATION

The first major cluster includes three subclusters. The first of these is composed of species of *Dipodomys* and *Perognathus* of North America, *Gerbillus nanus* of Iran, *Octomys* from Argentina, *Sekeetamys calurus* of Egypt, and *Meriones crassus* from Iran. The second subcluster includes heteromyids in the genera *Dipodomys* and *Microdipodops*, and the dipodids *Paradipus ctenodactylus* and *Eremodipus lichtensteini*. The third subcluster includes only dipodids—*Jaculus, Stylodipus,* and *Scirtopoda*.

The majority of species included within the first major cluster are bipedal (13/21), or have rather long hind feet (5/21). Most are seed eaters (19/21), although some, such as *Stylodipus*, are reported to take roots and tubers as well as seeds (Walker, 1964). *Octomys* from the Argentine Monte eats cacti, green vegetation, and, perhaps, large seeds (Mares, 1973), but its inclusion with what are mainly heteromyids is largely based on cranial (bullar inflation) and dental characteristics (Mares, 1976). Most of the species in the first major cluster have relatively short ears and long tails. Nevertheless, the first cluster is composed mainly of bipedal seed eaters with simple dentition, inflated bullae, relatively short ears, long tails, long hind feet, and which possess foot bristles. They are principally inhabitants of flatlands varying from sand to gravel, although such species as *Sekeetamys calurus* and *Octomys mimax* (which are clustered together), are rock dwellers.

The second major cluster generally includes medium-sized, quadrupedal herbivores. Thus, *Neotoma* and *Sigmodon* of North America are clustered with *Phyllotis* of Argentina, *Meriones libycus* of Iran, and *Psammomys obesus* of Egypt. The similarities of the North American species and *P. griseoflavus* have been discussed earlier (Mares, 1973, 1976). *Meriones libycus* feeds almost entirely on seeds (Naumov and Lobachev, 1975) and is included within this cluster largely on the basis of body size and body proportions. *Psammomys obesus* inhabits salty-clayey flats and builds extensive burrows under green vegetation in hummocks; it feeds on green vegetation (Walker, 1964; Wassif, 1972).

←

Fig. 23.—Correlation phenogram resulting from a cluster analysis of 78 desert rodent species utilizing 25 morphoecological characteristics.

Table 18.—*Mean Mahalanobis Distance (D²) of each desert fauna to all other faunas when 25 morphoecological traits are utilized (Fig. 21).*

	U.S.	South America	Australia	North Africa	South Africa	China	Russia	Iran
U.S.	19.9	35.0	81.2	29.0	31.0	48.0	47.0	38.3
South America	—	19.7	80.7	47.3	51.5	54.3	49.0	49.3
Australia	—	—	27.2	83.3	85.4	77.1	77.4	83.2
North Africa	—	—	—	23.5	28.8	52.3	51.6	41.2
South Africa	—	—	—	—	20.0	49.1	52.2	45.0
China	—	—	—	—	—	22.8	31.3	51.0
Russia	—	—	—	—	—	—	22.8	53.6
Iran	—	—	—	—	—	—	—	19.1

The third major cluster includes the dipodids (*Allactaga, Alactagulus, Pygeretmus,* and *Jaculus blandfordi*) and the jird, *Meriones persicus.* With the exception of *Meriones,* all are bipedal. All are apparently herbivorous.

The fourth major cluster is composed of sciurids, and includes *Ammospermophilus* of North America, *Geosciurus* of South Africa, *Xerus* of North Africa, and *Spermophilopsis* of the U.S.S.R. All are medium-sized, burrowing, scansorial herbivores-omnivores.

The fifth major cluster is composed of two distinct subclusters. The first contains the fossorial species clustered together in Fig. 22; *Octodontomys simonsi* is loosely joined to the fossorial group. The other subcluster includes medium-bodied herbivores, such as *Microcavia, Octodon, Ctenodactylus,* and *Rhombomys.*

The sixth major cluster is comprised of eight smaller clusters—the first includes *Onychomys, Calomyscus* and *Malacothrix,* which may be quadrupedal insectivores, or at least micro-omnivores (Mares, 1976); the second contains *Peromyscus, Baiomys, Gerbillus, Taterillus, Notomys,* and *Stea-*

tomys, largely omnivorous quadrupeds which may eat significant amounts of seeds; the third subgroup contains *Mystromys, Cricetulus,* and *Phodopus;* the fourth includes *Pachyuromys* and *Desmodillus,* while *Thallomys* is only loosely included within this subcluster; the fifth subcluster contains *Peromyscus, Reithrodontomys, Eligmodontia,* and *Petromyscus.* The final group of rodents completing the major cluster includes *Cricetulus barabensis, Dipus sowerbyi,* and *Leggadina delicata.*

The 27-character distance phenogram utilizing only non-ratio traits is shown in Fig. 24; the cophenetic correlation coefficient is 0.798. I will not discuss the individual OTU's at length. Basically this technique divides the rodents into four major groups—bipedal forms; quadrupedal species; fossorial species; and ground squirrels. In many ways there were no significant deviations in the 27-trait, non-ratio analysis, from those derived from the 40- and 25-traits analyses, although I believe that having all three analyses is an aid to understanding various aspects of the comparative biology of numerous species.

CONVERGENT EVOLUTION OF DESERT RODENTS

Although the various deserts examined in this paper contain a diverse array of desert rodents, the computer analyses indicate that one particular region is not as ecologically distinct from another distant region as one might have expected. The most diverse desert examined, from the viewpoint of the total number of broad adaptive categories of rodents it supports, is that found in the United States and northern Mexico (Table 19). Basically, my analyses indicate that there are nine major niche types (or guilds) represented among the world's desert rodents, including bipedal granivores, quadrupedal

granivores, micro-omnivores, medium-sized omnivores, small insectivores, fossorial herbivores, medium-sized herbivores, larger herbivores, and bipedal herbivores. It is important to note that, although most of these categories are represented within each desert region, they are not always filled by a rodent. It is not uncommon to find at least one member of each category present in any particular locality, and coexistence of species within one particular category is often seen (for example, Hoffmeister and Goodpaster, 1954; Chew and Chew, 1970; Rosenzweig et al., 1975; Brown, 1975). The

Dipodomys merriami
D. ordi
Microdipodops megacephalus
Dipodomys microps
Dipodomys agilis
D. spectabilis
D. deserti
Octomys mimax
Sekeetamys calurus
Octodontomys simonsi
Rhombomys opimus
R. opimus
Jaculus orientalis
J. deserti
Stylodipus andrewsi
Eremodipus lichtensteini
Scirtopoda telum
Paradipus ctenodactylus
Jaculus blandfordi
Neotoma albigula
N. lepida
Sigmodon hispidus
Phyllotis griseoflavus
Psammomys obesus
Meriones libycus
M. crassus
M. persicus
Dipus sowerbyi
Microcavia australis
Octodon degus
Ctenodactylus gundi
Allactaga mongolica
Pygeretmus shitkovi
Alactagulus pumilio
Allactaga elater
Perognathus baileyi
P. intermedius
P. penicillatus
P. flavus
Gerbillus nanus
Onychomys torridus
Calomyscus bailwardi
Peromyscus crinitus
Malacothrix typicus
Phodopus roborowskii
Cricetulus barabensis
C. curtatus
Notomys alexis
N. carpentarius
Taterillus harringtoni
Gerbillus campestris
Gerbillurus paeba
Peromyscus eremicus
P. maniculatus
Reithrodontomys fulvescens
R. megalotis
Steatomys athi
Petromyscus barbour
Eligmodontia typus
Baiomys taylori
Leggadina delicata
Cardiocranius paradoxus
Ammospermophilus harrisi
Myetromys albicaudatus
Thallomys nigricaudata
Pachyuromys duprasi
Desmodillus auricularis
Thomomys bottae
Ctenomys fulvus
Spalax ehrenbergi
Pappogeomys caetanops
Bathyergus janetta
Georhychus capensis
Cryptomys darlingi
Heterocephalus glaber
Xerus
Geosciurus
Spermophilopsis leptodactylus

1.7   1.3   .9   .5   .1
DISTANCE

great diversity of desert rodents in North America may be at least partially explained by the enormous fluctuation, fracturing, and reformation of xeric habitats in the Pleistocene (see Van Devender, 1977; Mares, 1979). Indeed, the only major niche type that is lacking in the New World is that of bipedal herbivore, a category that is important in the Old World, particularly in Russia and Australia.

The Monte, as has been noted, is quite depauperate in both number of species inhabiting the desert, and in abundance of individuals at a particular locality (Mares, 1976; Mares and Rosenzweig, 1978). Granivorous mammals are lacking entirely, although the overall array of niche types is not exceedingly narrow. The small insectivore niche, which is filled in North America by a rodent (*Onychomys*) and a shrew (*Notiosorex*) is represented by a marsupial mouse, *Marmosa pusilla*, which is rare, but regular, over much of the Monte (Mares, 1973). *Ctenomys*, fossorial caviomorphs, are close ecological analogues of the gophers of North America, while *Dolichotis patagona* is a large, cursorial rodent quite similar in morphology and ecology to the leporids of North America (Mares, Blair et al., 1977). *Microcavia* bears some ecological similarities to ground squirrels, and very likely fills a part of this niche category. It is strictly herbivorous, however, and thus not a perfect ecological equivalent, although in overall body proportions, habitat requirements, time of activity, and, perhaps, behavior, the two groups (ground squirrels and *Microcavia*) are similar (see Hawbecker, 1947; Hudson, 1962; Mares, 1973). A potential candidate for the medium-sized omnivore niche in the Monte is the armadillo, *Chaetophractus vellerosus*. This species eats a wide variety of plant and animal matter, and is a conspicuous element of the Monte Desert (Greegor, 1975; Mares, Blair et al., 1977).

The Australian desert, while supporting a low diversity of rodents, nevertheless has a rich mammal fauna, although most species are of low density (Watts, 1974; Morton, 1979). Five of the nine major guilds are represented in Australia, with two others perhaps partially represented. *Notomys* seems to fill the bipedal granivore niche, even though it was not clustered with bipedal rodents except when

←

Fig. 24.—Distance phenogram resulting from a cluster analysis of 27 non-ratio morphological characteristics.

Table 19.—*Suggested categorization of niche types of small mammals represented within each of the desert regions included in the preceding analyses. Although many species in the table were not included in the computer analyses, they are listed here for completeness.*

Rodent niche category	United States	Monte	Australia	North Africa	South Africa	Iran	Russia	China
Bipedal granivores	*Dipodomys* *Microdipodops*		*Notomys*	*Jaculus*		*Jaculus*	*Jaculus* *Paradipus* *Eremodipus*	*Stylodipus* *Jaculus*
Quadrupedal granivores	*Perognathus*			*Taterillus* *Pachyuromys* *Gerbillus* *Sekeetamys*	*Gerbillus* *Tatera* *Gerbillurus*	*Gerbillus* *Meriones*	*Meriones*	*Phodopus* *Meriones* *Brachiones*
Micro-omnivores	*Peromyscus* *Reithrodontomys* *Baiomys*	*Eligmodontia* *Andalgalomys* *Phyllotis*	*Leggadina* *Pseudomys*		*Desmodillus* *Petromyscus* *Dendromus* *Rhabdomys*	*Calomyscus*	*Cardiocranius*	*Cardiocranius*
Medium-sized omnivores	*Ammospermophilus* *Spermophilus*	*Chaetophractus*		*Xerus*	*Geosciurus* *Xerus*		*Spermophilopsis*	
Medium-sized herbivores (largely above-ground plant parts)	*Neotoma* *Sigmodon*	*Microcavia* *Octomys*	*Leporillus*(?)	*Psammomys* *Ctenodactylus*	*Paratomys* *Thallomys*	*Rhombomys*	*Rhombomys* *Scirtopoda*	*Rhombomys* *Cricetulus*
Small insect eaters	*Onychomys* *Notiosorex*	*Marmosa*	*Antechinus* *Sminthopsis* *Antechinomys* (*Notoryctes*)*	*Crocidura* *Calomyscus*(?)	*Crocidura* *Elephantulus* *Macroscelides* (*Eremitalpa*)* *Mystromys*	*Crocidura*	*Crocidura* *Salpingotus*	*Crocidura* *Salpingotus*
Fossorial herbivores	*Thomomys* *Pappogeomys*	*Ctenomys*		*Heterocephalus* *Spalax*	*Bathyergus* *Georlychus* *Cryptomys*			
Larger herbivores	*Sylvilagus* *Lepus*	*Dolichotis*	*Onychogalea*	*Lepus*	*Pedetes*	*Lepus*	*Lepus*	*Lepus*
Bipedal herbivores (largely underground plant parts)			*Caloprymnus* *Bettongia* *Lagorchestes*	*Allactaga*		*Allactaga*	*Dipus* *Alactagulus* *Allactaga* *Pygeretmus*	*Allactaga* *Euchoreutes* *Dipus*

* Fossorial insectivore.

analyses were limited to external traits alone (Mares, unpublished). Most analyses placed *Notomys* with various gerbils or micro-omnivores. It is likely that *Notomys* may not be as obligately granivorous as surmised (Morton, 1979) and may, in fact, exhibit a catholic diet including insects (for example, Watts, 1973). Medium-sized herbivores may be lacking in the Australian Desert, although *Leporillus* might fill this niche. It is known to take some animal matter, although most information regarding this species is anecdotal (Walker, 1964; Morton, 1979). Small insectivorous marsupials (some bipedal forms) are common in Australia, as are smaller, bipedal herbivores and larger herbivores. These latter two categories are represented by small rat kangaroos and wallabies. The fossorial marsupial mole, *Notoryctes*, is listed as a desert animal by Morton (1979) without data on its distribution or abundance; the species is apparently wholly insectivorous (Walker, 1964).

The North African fauna is the second most complex assemblage of desert rodents in the world. Many of the species may be quite abundant in particular localized areas (Mares, personal observation), and, in this respect as well as in overall diversity, this fauna resembles that of North America. The high diversity across this immense region may be due in part to a Pleistocene history of formation of desert refugia paralleling that which occurred in the southwestern United States (Schlitter, 1976). Bipedal granivores are represented by *Jaculus*, while various genera of quadrupedal granivores are common in the desert. As more is learned about the biology of the various species comprising the quadrupedal category, it would not be surprising to find that some are actually micro-omnivores; various analyses suggest that *Pachyuromys* and *Desmodillus* may include animal matter in their diet. The highly desert specialized sciurid, *Xerus*, fills the medium-sized omnivore niche that, in deserts, is apparently limited to squirrels. *Psammomys* and *Ctenodactylus* seem to fill a role similar to the wood rats of North America and the cavy of the Monte; indeed, there is a pronounced morphological resemblance between the cavy and the ctenodactylid. Two genera of fossorial herbivores (*Spalax* and *Heterocephalus*), strongly convergent upon other species filling a similar role in other deserts, inhabit northern and eastern Africa. The morphological convergence associated with extreme fossoriality is well known (McNab, 1966), and similar-

ities probably extend to behavioral and other ecological attributes as well. The small, bipedal herbivore category is represented by *Allactaga tetradactyla* which occurs in far northern Africa in a very limited geographical area (Setzer, 1956; Hoogstraal, 1966; Ranck, 1968; Harrison, 1972). Finally, as in North America, the large rodentiform herbivore of North Africa is the hare, *Lepus,* a role filled by a wallaby in Australia and a rodent in the Monte. Even the gaits of these hopping-cursorial herbivores in the widely-separated deserts are somewhat similar. The shrew, *Crocidura,* is known to frequent xeric habitats, and is the small insectivore of the Sahara (Wassif and Hoogstraal, 1953; Setzer, 1956; Hoogstraal, 1962). No small insectivorous rodents are known in the Sahara, although larger insectivores, hedgehogs of the family Erinaceidae (*Paraechinus*) are common in the desert (Setzer, 1956; Hoogstraal, 1962), and seem similar to the Monte armadillos, trophically, in their burrowing habit, and in overall body proportions.

Southern Africa is the only desert, besides the Monte, which lacks bipedal granivores; small, bipedal herbivores are also missing in this desert. All other categories are represented, however. *Gerbillus* (and, perhaps, *Desmodillus*) are the quadrupedal granivores, while *Petromyscus, Dendromus, Rhabdomys* and perhaps, *Desmodillus,* are micro-omnivores (see Walker, 1964; Nel and Rautenbach, 1975; Nel, 1978). *Geosciurus* is the medium-sized omnivore, and *Paratomys* and *Thallomys* are the medium-sized herbivores; the latter with its arboreal tendency, recalls *Phyllotis griseoflavus* of the Monte, and *Neotoma* of the United States (see Walker, 1964; Mares, 1973; Nel and Rautenbach, 1975; Nel, 1978). *Mystromys* is suggested in a number of computer analyses as possibly filling a small insectivore role, or that of a micro-omnivore, in southern Africa. Various insectivores are known from xeric regions in southern Africa, however, including *Crocidura* and two genera of elephant shrews (Family Macroscelididae), *Elephantulus* and *Macroscelides* (Bigalke, 1978; Nel, 1978); the latter two genera are saltatorial (Walker, 1964). Golden moles (Family Chrysochloridae), fossorial insectivores, are also known from xeric habitats in this region (Walker, 1964; Rautenbach, 1978). The larger herbivore of southern Africa is the springhare (Family Pedetidae), *Pedetes,* feeding on both above- and below-ground plant parts (Walker, 1964). Sciurids are present in southern Africa, and fosso-

rial herbivores (Family Bathyergidae) are also common (Walker, 1964; Rautenbach, 1978).

The desert of Iran presents one of the poorest deserts from the number of genera of small mammals occurring in arid areas; nevertheless, seven of the nine niche categories are represented. Species of *Jaculus* are the bipedal granivores, while *Gerbillus* and *Meriones* are quadrupedal granivores (Naumov and Lobachev, 1975). Computer analyses imply that *Calomyscus* is a micro-omnivore, while *Rhombomys* is the medium-sized herbivore (Lobachev and Khamdamova, 1972). *Allactaga* is the bipedal herbivore, while fossorial herbivores and medium-sized omnivores are lacking in the arid areas (Lay, 1967). *Lepus* is the large herbivore, as it is throughout Asia.

The ecology of the small mammal fauna of the Russian desert has been greatly clarified by Naumov and Lobachev (1975). This desert is quite complex faunistically, rivaling both the Sahara and North American deserts. Three genera are included as bipedal granivores, although two of these, *Paradipus* and *Eremodipus*, may actually be more herbivorous than granivorous (Walker, 1964; Naumov and Lobachev, 1975). Various species of *Jaculus*, however, are primarily granivorous. Many species of *Meriones* are present over this desert as quadrupedal granivores. *Cardiocranius paradoxus*, a species which is poorly known ecologically, is possibly a bipedal micro-omnivore, although Naumov and Lobachev (1975) suggest seeds are the only food. *Salpingotus*, a near relative of *Cardiocranius*, and also a bipedal species, may fill the role of small insectivore. The ground squirrel, *Spermophilopsis*, fills the medium-sized omnivore niche, while *Rhombomys* and, perhaps, *Scirtopoda* are the medium-sized herbivores (Lobachev and Khamdamova, 1972; Naumov and Lobachev, 1975). No fossorial herbivores are present in the Russian desert, while *Lepus* is the large herbivore. The most diverse guild in this desert is that of the small bipedal herbivores, having no fewer than four genera represented (*Dipus, Alactagulus, Allactaga, Pygeretmus*), and perhaps as many as six, if *Paradipus* and *Eremodipus* feed largely on roots and tubers.

The Chinese desert system is largely unstudied (Lowe, 1968), but generally it is quite similar to the Russian desert. Seven of the adaptive categories are represented with only fossorial herbivores and ground squirrels being absent. There are fewer genera of dipodids than in Russia, but they neverthe-

less contribute bipedal granivores (*Jaculus, Stylodipus*), a micro-omnivore (*Cardiocranius*), an insectivore (*Salpingotus*), and bipedal herbivores (*Allactaga, Euchoreutes, Dipus*) to this desert.

Clearly, there are great similarities in the types of niche categories represented in each desert. No desert supports all nine categories although the deserts of North America, North Africa, and Russia (Turkestan Desert), each have eight. Usually these are filled by rodents, but a perusal of Table 19 indicates that there is great plasticity present in the small mammals evolving in a particular desert region, whatever their taxonomic composition. Thus, for example, the small insect eater niche is filled by a shrew and a rodent in North America, a marsupial mouse opossum in the Monte, various marsupials in Australia, elephant shrews, a soricid, and perhaps a rodent in southern Africa, a shrew in North Africa, and a shrew and a rodent in the Turkestan and Gobi deserts. Some of these insectivores are quadrupedal, two are burrowing (a marsupial and a golden mole), and some are bipedal (elephant shrews and a rodent).

Bipedal and fossorial herbivores seem to be mutually exclusive within a desert region, with the exception of *Allactaga* in northern Africa (where *Spalax* is present). *Allactaga* is a fairly recent colonizer of Africa, however, and has a very small geographic distribution (Ranck, 1968). Apparently, as a desert develops, a group of rodents can opt for fossoriality and a diet of underground plant parts, or can specialize on the same food resource by being bipedal (a strategy also employed by marsupials). Typical examples of the former adaptation are geomyids in North America, or bathyergids in southern Africa, while dipodids are the only bipedal root-eating rodents. Only one or the other strategy will predominate in any one desert, however.

Large herbivores in deserts are all specialized for rapid, rather long-distance, locomotion; some are cursorial, others bipedal. Each desert generally supports only one genus and species per locality within this category; coexistence of species is the exception (*Sylvilagus* and *Lepus* in North America) rather than the rule.

Medium-sized herbivores are found in each of the deserts of the world. They are often arboreal or limited to localized areas of dense (often halophytic) vegetation. They are almost always quadrupedal, with the exception of *Scirtopoda*, whose inclusion in this category is uncertain.

Micro-omnivores and medium-sized omnivores are present in most deserts. The latter are usually sciurids, and the inclusion of *Chaetophractus* of the Argentine Monte is only to illustrate that a medium-sized omnivorous armadillo may fill part of the squirrel niche in that desert. Iran and China lack desert squirrels and this may be because either insects and/or the usual seed and fruit resource is in short supply. Certainly the arboreal diversity of Iranian arid areas is exceedingly low.

Quadrupedal and bipedal granivores are usually present within each desert, although the Monte and Australia lack the former, and the Monte, southern African and, perhaps, Australian deserts may lack the latter. Bipedal granivores are always rodents and usually medium-sized species (in the 30–150 g body size range), whereas quadrupedal granivores may include smaller species (for example, *Gerbillus, Perognathus*).

Micro-omnivores are always rodents and almost always quadrupedal (with *Cardiocranius* being a possible bipedal exception). They are present in probably all major desert areas and often represented by more than one genus within a desert.

Bipedality occurs in all deserts except the Argentine Monte. It may be found in any food category, although it is most common in species eating seeds, insects, and underground plant parts. It seems to be associated with sparse vegetation cover, although bipeds and quadrupeds usually live sympatrically in most deserts. The Turkestan (U.S.S.R.), Chinese (Gobi), and Australian deserts have the greatest diversity of bipedal small mammals, with four of the major niche types represented by bipedal species.

From the preceding analyses, I suggest that, given time and opportunity, rodents will evolve to fill particular guilds in desert ecosystems. In deserts where it is known that rodents were late colonizers (Monte, Australia), these same guilds were filled by marsupials. Few deserts have unoccupied guilds, however, and it is likely that future evolution within these deserts will be that of refinement within a guild, rather than the development of a new, unexploited adaptive zone. Only in the Monte and in Australia do there seem to be vacant zones awaiting exploitation by rodents. Given the evenness with which such zones have been filled in other desert areas, I feel that the evolution of such species in these deserts is highly probable.

Schall and Pianka (1978) discussed convergent evolution in general terms and concluded that there is much evidence, both theoretical and empirical, suggesting that communities do not converge, although they point out that spectacular incidents of convergent evolution do occur occasionally. I believe, however, that there is much evidence, both theoretical and empirical, that communities do converge (for example, Cody, 1974; Fuentes, 1976; Orians and Solbrig, 1977; Cody et al., 1977). The similarities in the plant communities of the Sonoran and Monte deserts, or of the Chilean and Californian chaparral scrub areas are indeed remarkable; most deserts have similar physiognomies. Also, there are many examples of broad similarities in vertebrate and invertebrate communities in xeric areas. Ecologists have often looked for the differences in communities around the world rather than the similarities. Thus, one with experience in the Sonoran Desert is apt to notice a *Rhea* in the Monte as a remarkably odd species, and not reflect on the great similarities between the rodent *Dolichotis* and Sonoran jackrabbits. Also, the presence of a small mammalian desert insectivore in various deserts, whether it be a marsupial, such as *Sminthopsis* in Australia, *Marmosa* in Argentina, a shrew (*Notiosorex*) in the Sonoran Desert, a rodent (*Onychomys* or *Calomyscus*) in the Sonoran or Iranian deserts, or even an elephant shrew (Macroscelididae) in Africa, suggests that there are niches in deserts that are best filled by mammals, if mammals have had sufficient evolutionary time to evolve the necessary adaptations. The preponderance of granivory and bipedality among small desert mammals needs no further demonstration. These adaptive strategies have evolved repeatedly in disjunct deserts in unrelated groups. Future research should center on the selective forces that channel adaptations into a broad suite of adaptive strategies. Deserts are severe environments for a small mammal. For those species which make an evolutionary hurdle into a new xeric-adapted mode, immense areas and abundant food resources supporting few other mammals become available for exploitation.

Convergent evolution should not be examined with the goal of finding a one-to-one correspondence of species (that is, niches) in disjunct areas, rather the entire array of adaptations employed by organisms inhabiting a biome should be examined. Three enormously diverse mammalian orders, the Marsupialia, Insectivora, and Rodentia, have developed numerous desert species that fit within a relatively few adaptive moulds; these species are often uncannily-similar morphologically, trophical-

ly, ecologically, and physiologically. Unique adaptations or ways of life are to be expected in species which often differ enormously in their genetic stock, but it is indeed interesting that, given these genetic differences, so many adaptations have evolved to endpoints that are so similar. Selection of one particular ecological zone early in the history of a taxon seems to canalize the adaptations that will develop along a relatively narrow evolutionary pathway. Such an occurrence suggests overriding similarities in selective forces within similar ecosystems, and suggests that the evolutionary options open to organisms inhabiting a desert (and, presumably, other ecosystems as well) are limited. As investigations of convergent evolution continue, and they are only in their infancy at the moment, we should begin to get a much deeper understanding of the evolutionary process, and the possible limitations to the diversity of modes of existence.

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APPENDIX 1

Annotated list of morphological characters utilized in multivariate analyses

1. *Head-body length.*—Distance from tip of snout to beginning of tail, generally derived by subtracting length of tail (vertebrae) from total length (tip of snout to tip of tail).

2. *Tail length.*

3. *Hind-foot length.*—From back of heel to tip of longest toenail.

4. *Height of ear from notch.*

5. *Length of longest vibrissae.*—A millimeter ruler was placed at base of vibrissae and the longest was measured to the nearest millimeter.

6. *Length of hair between shoulders.*—Measured by placing millimeter ruler against skin and noting length of majority of hairs.

7. *Tail/head-body ratio.*—The tail functions as an organ of balance, and would be expected to be particularly important to bipedal species. Arboreal species would also have need of a long tail for balance while climbing over branches.

8. *Hind foot/head-body ratio.*—Long hind feet relative to body size are often adaptations for a bipedal habit, as evidence by kangaroos, to cite an extreme example. Bipedality is a desert rodent adaptation, thus desert species would be expected to have a high hind foot to head-body ratio.

9. *Ear/head-body ratio.*—Mammals in deserts have two ways of increasing audial acuity. First, pinnae can be greatly enlarged, resulting not only in greater hearing ability, but in an efficient organ for radiating body heat to the environment (see Schmidt-Nielsen, 1965, regarding *Lepus*). Secondly, species can evolve inflated tympanic bullae to increase sound reception. It is possible that non-fossorial species would tend toward larger ears, particularly if they were diurnal in activity. Species which live in burrows might find long ears a handicap in narrow tunnels and would thus tend toward inflated bullae (for example, Webster, 1962; Lay, 1972). *Lepus* (jackrabbits and hares) is an example of non-fossorial species having long ears, and *Dolichotis* (the Patagonian "hare") a species which lives in burrows and possesses shorter ears.

10. *Vibrissae/head-body ratio.*—Possibly long vibrissae are associated with desert living for a number of reasons. Desert rodents, known to be very nocturnal even to the point of avoiding moonlit nights (for example, Lockard and Owings, 1974), could facilitate moving about on a pitch-black evening by utilizing long and dense vibrissae. The open habitat of a desert would be conducive to long vibrissae, whereas an animal such as a microtine which lives in dense vegetation or a fossorial animal might not reap selective advantage by having exceedingly long vibrissae which would be in constant contact with vegetation or burrow walls.

11. *Hair/head-body ratio.*—Ratio of the length of hair between shoulders to head-body length. I would not expect desert species to have either particularly long or short hair, whereas species from colder localities, such as a coniferous forest, might possess fairly long pelage for greater insulation.

12. *Weight.*—Measured to 0.1 grams.

13. *Foot bristles.*—Coded none (0), somewhat (1), many and well developed (2), stiff and specialized (3), brush-like (4). This character offers an example of the distinction between an ecological character and a taxonomic one. The fossorial rodents *Thomomys* and *Ctenomys* possess stiff bristles between the toes which facilitate soil movement. *Thomomys* pushes soil from its burrow by a forward motion of the body and forefeet and possesses bristles between the toes of the front paws. *Ctenomys*, on the contrary, pushes soil with the posterior parts of the body and by rapid backward kicks with the hind feet whose toes have stiff bristles. Were one interested in taxonomic characters, occurrence of bristles at different ends of the body could differentiate the species. Being interested primarily in ecological function, however, in this study only the presence of these functionally similar structures was noted, not their location on the body.

14. *Tuftiness of tail.*—Coded from no tuft (0) to large, well-developed, conspicuous tuft (5). Why many desert rodents have tufts at the ends of their tails is unclear. Possibly it functions as a balancing structure, although I doubt the weight of the tuft is sufficient to function in this manner. Increased resistance as it

moves through the air could make the tuft act as a rudder to allow the animal more easily to flick its body sideways in mid-air. More plausible perhaps is a predator-distraction function of a large white tuft. If the predator's attack could be deflected to this point, and if the tail were easily autotomized (as Layne, 1972 has shown for *Peromyscus floridanus*), the possibilities of an animal's escaping would be greatly increased.

15. *Basal length* (modified).—From the anterior inferior border of the foramen magnum to the anterior parts of the premaxillary bones, not necessarily in the midline of the skull (Fig. 25).

16. *Incisor-molar length.*—Length of line connecting posterior margins of alveoli of upper incisors with posterior margin of molariform tooth row occlusal surface. Such a measure gives an idea of overall length of the "masticating area" of the mouth (Fig. 25).

17. *Bullar length.*—Length of straight line connecting anterior point of insertion of bulla into basilar region of skull with posterior point of bulla evident when the skull's basilar region is facing upward (Fig. 25).

18. *Bullar width.*—Straight-line distance approximately perpendicular to bullar length line connecting widest points of upward-facing bulla (Fig. 25).

19. *Width across molariform tooth rows.*—Length of straight line connecting right and left labial margins of tooth rows at their midpoints. This character gives an indication of mouth width much as character number 16 measured mouth length (Fig. 25).

20. *Zygomatic breadth.*—Greatest distance across zygomatic arches, at whatever point along the arch at which distance was maximal. The line is perpendicular to the long axis of the skull. This measure gives some idea of width of skull, greater width often being associated with animals which are heavy and powerful (Fig. 25).

21. *Incisor width.*—Width measured across both incisors just above point where tapering begins, or, on those that do not taper, at tip of incisors. Hershkovitz (1962) noted the tendency of triturating incisors to be thick and powerful (Fig. 25).

22. *Incisor length.*—Straight-line distance connecting distal portion of incisor with its point of exit from the premaxillary bone. Species having seizer-digger incisors often have long, slender incisors (Fig. 25).

23. *Incisor-molar length/basal length × 100.*—Relative mouth length, size removed as a confounding factor.

24. *Bullar index = bullar length × bullar width/basal length.*—Index of bullar inflation.

25. *Length of molar tooth row (TRL).*—Length of occlusal surface of molariform teeth, from anteriormost to posteriormost points (Fig. 25).

26. *TRL/incisor-molar length × 100.*—Relative proportion of mouth composed of grinding teeth. I expect that a species such as the vole *Microtus,* for example, which consumes such silicacious materials as grass, might need larger molariform tooth rows to allow for a larger grinding area over which to crush this material. Seeds, which are eaten by many desert specialists, would not necessitate a large grinding surface.

27. *Width across tooth rows/basal length × 100.*—Relative width of mouth.

28. *Zygomatic breadth/basal length × 100.*—Relative width of zygomata, an indication of relative breadth of skull.

29. *Incisor width/basal length × 100.*—Relative incisor width.

30. *Incisor length/basal length × 100.*—Relative incisor length.

31. *Incisor angle.*—Coded from very proodont (0) to very opisthodont (5). Hershkovitz (1962) discussed many rodent incisor
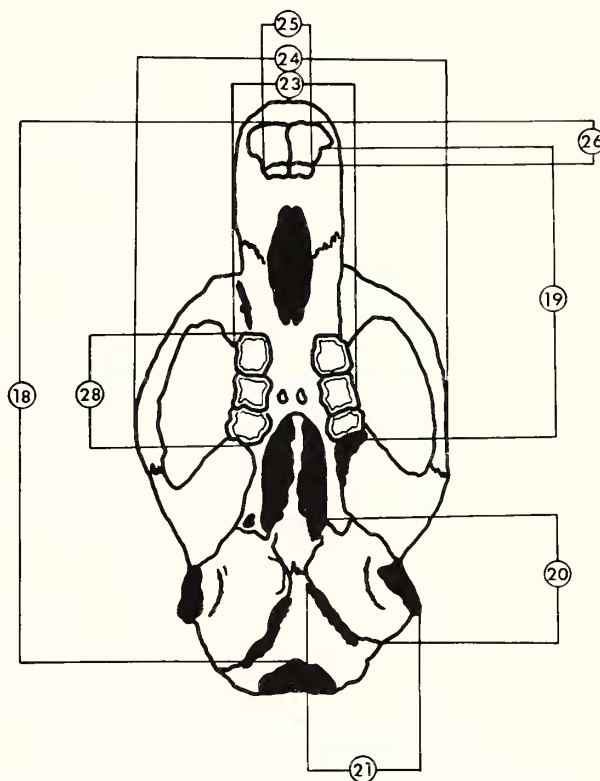

Fig. 25.—Cranial measurements used in the various multivariate analyses.

types. I would surmise that incisor angle can reflect diet somewhat. Grass-clipping *Sigmodon* and *Microtus* possess orthodont incisors, whereas granivorous heteromyids have incisors which are markedly opisthodont. Inflexion of the incisors may increase biting force on the tip such that greater efficiency at husking seeds results.

32. *Seizer-digger incisors.*—Hershkovitz (1962) defined this type of incisor as being generally slender and proodont, and functioning as a tool for digging up worms, insects, or roots. Some *Thomomys* possess such incisors and use them in digging burrows and roots. Coding: not a seizer-digger incisor (1) to very much so (3).

33. *Triturator incisors.*—Coded from not a triturator (1) to a very pronounced triturator function (3). Hershkovitz (1962) noted these incisors are used in gnawing and chopping and as hoes in digging. They are generally heavy and well-pigmented.

34. *Molar planation.*—Coded from crested molars (1) to planar molars (4). Hershkovitz (1962) remarked on the evolutionary stages involved in the change from primitive crested molars to specialized planar types. He also suggested such planation is correlated with increasing hypsodonty. Planar molars have a grinding or crushing function rather than the tearing and cutting inherent in the occlusion of the ridges, cusps and valleys of crested molars.

35. *Molar complexity.*—Coded from complex pentalophodont molars (0) to simple cylindrical teeth (6). Grassland and desert species have tended to evolve simple, cylindrical molariform molars. It would be expected that a species specializing on

tough, fibrous material would need not only planar teeth, but quite a complex system of enamel ridges in order to expose the hardest tooth material to the grinding of the vegetation. Complexity might even be increased by the formation of many enamel triangles (see triangulation, below) which would make the grinding of vegetation even more efficient. Granivorous desert species, on the other hand, could minimize enamel surface and simplify molariform teeth such that a basin is formed in which soft, husked seeds could be crushed.

36. *Tubercular hypsodonty.*—Coded from none (0) to pronounced (4). As Hershkovitz (1962:89) defined tubercular hypsodonty, it is the ". . . elongation of the coronal tubercle, or tubercles, at the expense of the remainder of the tooth, including the root. This type of hypsodonty is an adaptation for seizing, grasping, cutting, chopping or cracking." When this occurs among molariform teeth, it is often an indication of an insectivorous diet (vespertilionid bats, for example). Presence of tubercular hypsodonty in *Onychomys* is associated with its insectivorous diet.

37. *Coronal hypsodonty.*—Coded from none (0) to pronounced (3). The grazing habit is characterized by these grinding and crushing teeth, whereas species such as generalized forest dwellers (for example, *Peromyscus*) have not developed this molariform type.

38. *Molar triangulation.*—Coded from none (0) to pronounced (3). See Molar Complexity above.

39. *Molar tooth row width.*—Width of one molar tooth row (occlusal surface) at midpoint of the row.

40. *Relative molariform surface area.*—(Two times the molar tooth row width × molar tooth row length)/basal length. If indeed a grazer needs more surface area than a seed eater because of the tough dietary regimen, then the index should reflect food habits to some extent.

41. *Vibrissae density.*—Coded from low density (1) to very dense (4). See Vibrissae/head-body ratio above.

APPENDIX 2

Multivariate Analyses and Ratio Traits

Recently a number of questions have been raised regarding the use of ratios in certain multivariate tests (Atchley et al., 1976; Atchley and Anderson, 1978; Atchley, 1978; and others). Opposing points of view have been rendered by Corruccini (1977), Dodson (1978), Albrecht (1978), and Hills (1978). The comments of Atchley and his colleagues regarding the use of ratios in such techniques as principal components analysis, canonical variates analysis, canonical correlation analysis, and so on, are based on the underlying assumption that the data used in such analyses are multivariate normally distributed (m.n.d.). Ratios are usually employed in an attempt to scale the data for some common allometric relationship such as body size effects, which may be an overriding element in the different data sets (for example, Goodman and Paterniani, 1969; Goodman, 1972; Findley, 1972; Nevo, 1973; Karr and James, 1975; Mares, 1976; and many others). Part of the problem is that some of the mathematical steps leading up to the multivariate analysis are based on the assumption of a normal distribution, particularly such analyses as the formation of a similarity matrix based on product moment correlations (Pearson's r), or when data are standardized prior to being treated for conversion to such values as canonical loadings, etc. (Clark, 1975). Daultrey (1976:41) states, "Principal components does not require the data to be normally distributed; the use of Pearson's r *does*." He suggests that other correlation coefficients (for example, Spearman's rank correlation coefficient) be used where the m.n.d. of data is questionable. Cooley and Lohnes (1971:38) note that although a m.n.d. of data is necessary for many significance tests, and that the marginal distributions of the various data sets can be checked, normalizing the non-normal data sets may help, but caution that "normal marginals do not themselves guarantee an m.n.d., and we do not know of any useful test for multivariate normality." Various involved tests of normality have been outlined (Gnanadesikan, 1977), but I am not familiar with any paper dealing with a multivariate analysis of complex data sets that has first tested for complete multivariate normality of all of the data.

The arguments of Atchley and his coworkers are compelling, particularly if the level of significance of the various multivariate tests is important. Ito (1969) notes that violation of the multivariate normality requirement may be compensated for by a large sample size as far as testing hypotheses about mean vectors, but is not compensated for when data are employed in a variance-covariance matrix. Tatsuoka (1971) notes that the m.n.d. is a requirement for the strict validity of significance tests, but Blackith and Reyment (1971) consider significance testing of little value in biological data, and, indeed, suggest that most multivariate techniques are sufficiently robust to allow their basic assumptions to be violated to an extent (see also Crovello, 1970; Klecka, 1975; Robinson and Hoffmann, 1975). As far as transforming non-normal data to a normal distribution, Clifford and Stephenson (1975) suggest that the statistical transformations required to conform to strict normality may result in the loss of the "ecological sense" of the data.

Rohlf and Sokal (1965) and Sneath and Sokal (1973:147, 153) suggest the use of ratios to scale data, even though the frequent departure of ratio data from normality has been known for many years (for example, Pearson, 1897). Presumably they feel that violations of the m.n.d. assumption in multivariate analyses can be tolerated to a degree. Schnell (1970*a*, 1970*b*) used ratios in principal components analysis and found that analyses based on ratios reflected earlier classical taxonomic assumptions about the particular taxon he was studying (the suborder Lari). He found (1970*a*:48) that "As before" (when non-ratio traits were used) "the gulls, terns, and skimmers are separated by a fairly distinct gap. However, dividing by the Sternum Length had the additional effect of separating the skuas from the gulls." Further (Schnell, 1970*b*:294), "When correlated characters are used" . . . one should transform the ". . . character space (such as by the use of ratios) before clustering to reduce the effect of a general trend in characters, such as a general size factor . . ." which ". . . would make the resulting phenogram a possible candidate for a general phenetic classification." Although Atchley has

shown that in some cases ratios are actually *more* correlated with the factor supposedly being removed via the use of the ratio, other workers (Corruccini, 1977; Lemen and Findley, manuscript) have not found this to be the case. Undoubtedly more work remains to be done in this area (see also Oxnard, 1978).

Multivariate analyses apparently have been successfully performed on data which are qualitative in nature and which obviously violate the assumption of adherence to the m.n.d. (Miller and Butler, 1966), but as Bennett and Bowers (1976:118) point out "If the purpose of a particular factor analysis on qualitative data is simply to identify clusters of similar variables, then analysis of such matrices may be satisfactory."

There is little doubt that Atchley and his coworkers are correct in their strict interpretation of having the data conform to *all* of the assumptions of the various multivariate procedures (something that is seldom, if ever, done), and this is certainly necessary if an investigator is interested in attaching a precise level of significance to his results, but it does not seem to be true for a general understanding of the interrelationships of the various factors that are included in a multidimensional analysis of the data. As Cooley and Lohnes (1971:38) point out, "The hazards of overfitting in multivariate analysis are great. Although significance tests, when appropriate, can help to protect against reporting results that can never be replicated, we tend to treat our multivariate models as primarily heuristic rather than inferential procedures."

In earlier papers (Mares, 1975b, 1976), I have attempted to use multivariate analyses of numerous morphological traits (including some ratios) as a heuristic tool to attain a preliminary assessment of convergent characteristics among disparate desert rodent taxa. I continue that line of reasoning in this paper bearing in mind that the use of ratio characters may limit the degree of precision of the data in certain analyses. In the past, results of such analyses had fit quite well with my interpretations of the ecological relationships of the rodents which were obtained from various other research techniques (for example, comparative physiological investigations, natural historical studies, food habits analyses, etc.). As is evident in this report, the use of such techniques has also led to counterintuitive interpretations that appear to have merit.